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DEDICATED TO THE MEMORY OF

DR. JOHN E. POTZGER

1886-1955

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JOHN E. POTZGER 1886-1955

By

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If there has ever been a story to inspire a new generation of students to do great things, it is the story of John E. Potzger. Here was a man who literally overcame every obstacle. His enthusiasm, scholarship, and hard work brought success in the form of lasting contributions to our knowledge of the world and in students who will carry on his work. It is men like Professor Potzer who make a university great; Butler University can take pride in the fact that it was here that his scientific career started, grew, and developed into maturity.

John Ernest Potzger was born in Presque Isle County, Michigan, on July 31, 1886. His father was a Lutheran minister in what was then backwoods lumbering country. He grew up with a love of the forest and a respect for the value of hard work which were to result so many years later in his career as a forest ecologist and an interpreter of the vegeational history of this North Woods he knew so well.

But many things stood between him and that seemingly predestined goal which even he did not see for so long—brief schooling in the primitive classrooms of the forest country, a five-year struggle for an education at the Lutheran Teachers College, and then 24 years as a teacher of music and leader of young people in the Lutheran Day School of Indianapolis. During all of this time, he kept up his interest and training in music, studying under some of the best piano teachers of the day. In addition, he was attending night classes at Butler with the idea of getting an A. B. in languages. It was here that he reached a turning point in his life that was as unexpected as it was significant. To satisfy the science requirement for graduation, he enrolled in 1925 in the general botany class of the late Dr. Ray C. Friesner. The effect was immediate—a decision to become a botanist and to start an entirely new career at an age when so many persons are self-satisfied and even looking forward to retirement. The finishing of the bachelor's degree and a master's degree at Butler and the attainment of a Ph. D. degree at Indiana University were still to take seven more long years but he went at it with all the enthusiasm and drive of a young graduate student. Here in the field of plant ecology was something challenging and new and there were several whose influence on him in those days served to speed him on his way—Ray C. Friesner, Stanley A. Cain, Frank C. Gates, among others.

In the spring of 1932, he received his doctor's degree at Indiana University

and that fall, he returned to the Butler campus as an instructor in botany. The Butler Botany Department was a lively place with its usual quota of enthusiastic students already inspired by Friesner and Cain. It took a good man to step in there and lead—and that is just what the new Dr. John Potzger did. Those of us who were privileged to be his students then will never forget that year with his patient guidance in the laboratory and dynamic leadership in the field. This was just the start of his 23 years of teaching at Butler which led eventually to his chairmanship of the department after the death of Dr. Friesner in 1952.

It was not only in teaching that Dr. Potzger was to excel. Still to come were his substantial contributions to palynology, the science of pollen analysis. While his work on Indiana vegetation has added much to the knowledge of successional dynamics and climax structure of the deciduous forest, it was in the study of postglacial succession as brought out by pollen analysis that he was happiest. This pollen period began about 1940 and dominated the rest of his life. The summers were spent boring bogs all over the north country from Minnesota to Quebec and Maine, and during the winters the millions of pollen grains were studied and counted. As a result, we know much more of what happened to vegetation during and after the Pleistocene glaciation than we did just fifteen short years ago. Not only is postglacial succession better understood, but along the way came new ideas on lake filling and bog development and new techniques for the difficult business of getting fossil pollen samples from the bottom of lakes and out of the peats of bogs. There were many others working on these same problems but he was always a leader. His marriage in 1947 to Esther Whitney gave him a cheerful co-worker whose help and encouragement were invaluable in these busy years.

Dr. Potzger in his relatively short professional life thus came to be one of the outstanding American ecologists. He was a hard worker in the committees and projects of the Ecological Society of America and in 1953 he was honored by being elected its President. During the last two years of his life, he was constantly at work not only on the affairs of the Society but in the teaching laboratories at Butler and in the lakes, bogs, and tundra of Quebec where his headquarters were at the Mont Tremblant Field Station of the Service de Biogeographie of the University of Montreal. He was everywhere and seemingly doing everything—it was not at all unusual to receive a long-distance call from some remote Quebec village when he had an idea that would help the Society.

He returned from Canada in September, 1955, to attend the Society's meetings at East Lansing, Michigan, and to give his presidential address. It was his last service to the Society and his message was typically one of enthusiasm and new information. He was full of plans for new work and new places. His death just a few days later on September 18 came as a great personal loss to many botanists and to American ecologists particularly. There are many whom he helped

with a word of encouragement or a sound piece of advice; they will always miss him. Nevertheless, the seeds which his work planted will continue to grow in many ways and man's understanding of nature will always be better because of what he did.

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POLLEN STUDY IN THE GATINEAU VALLEY, QUEBEC[1]

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The authors have repeatedly made reference to the complexity of Quebec's past glacial and forest history, determined in part by the wasting Laurentide ice center, sea invasion, large pre-glacial lakes, altitudinal differences between the Shield and the St. Lawrence valley, as well as by the developments in the history of the Great Lakes.

In this maze of controlling influences, the Ottawa valley is unique in its extension from the St. Lawrence valley a great distance northward into the Shield. As one flies over rivers in the James Bay area today, one is impressed with the influence which valleys have on forest migrations. It is quite evident that these valleys are today centers of distribution for forests which later fan out over the whole area. In early post-glacial times, the Ottawa valley may likely have been such an avenue for migration northward as well as into the rugged Shield. For that reason a pollen study was begun in the Gatineau valley, a tributary of the Ottawa river (Fig. 1), to see if the forest might give some information on differences in forest and climate as compared with areas on the Shield.

GLACIAL HISTORY

According to Antevs (1) the wasting Mankato ice left a prominent outwash plain and moraine in the neighborhood of Kazabazua, which he calls the Lake Timiskaming Retreat, halting at the Cochrane moraine, 150 miles south of James Bay. This he considers correlative with the close of Lake Algonquin. At that time trees could begin their northward march and invasion of the region called Quebec.

METHODS

Samples were taken at 1-foot or more frequent intervals with the Hiller borer. These samples were placed into properly labelled vials and stoppered. In the laboratory the Geisler (3) alcohol method was used when compacted sediments separated readily, and the Erdtman (2) KOH method was used with compacted sediments. Gentian violet served as stain. One hundred and fifty to 200 pollen grains were counted at each level. Only pollens of trees were used to construct the graphs (Figs. 3, 4) but pollens of shrubs and herbs were tabulated and are given as total numbers counted in Tables 1-5.

[1] Owing to the recent death of Dr. Potzger correspondence relating to this paper should be directed to Albert Courtemanche.

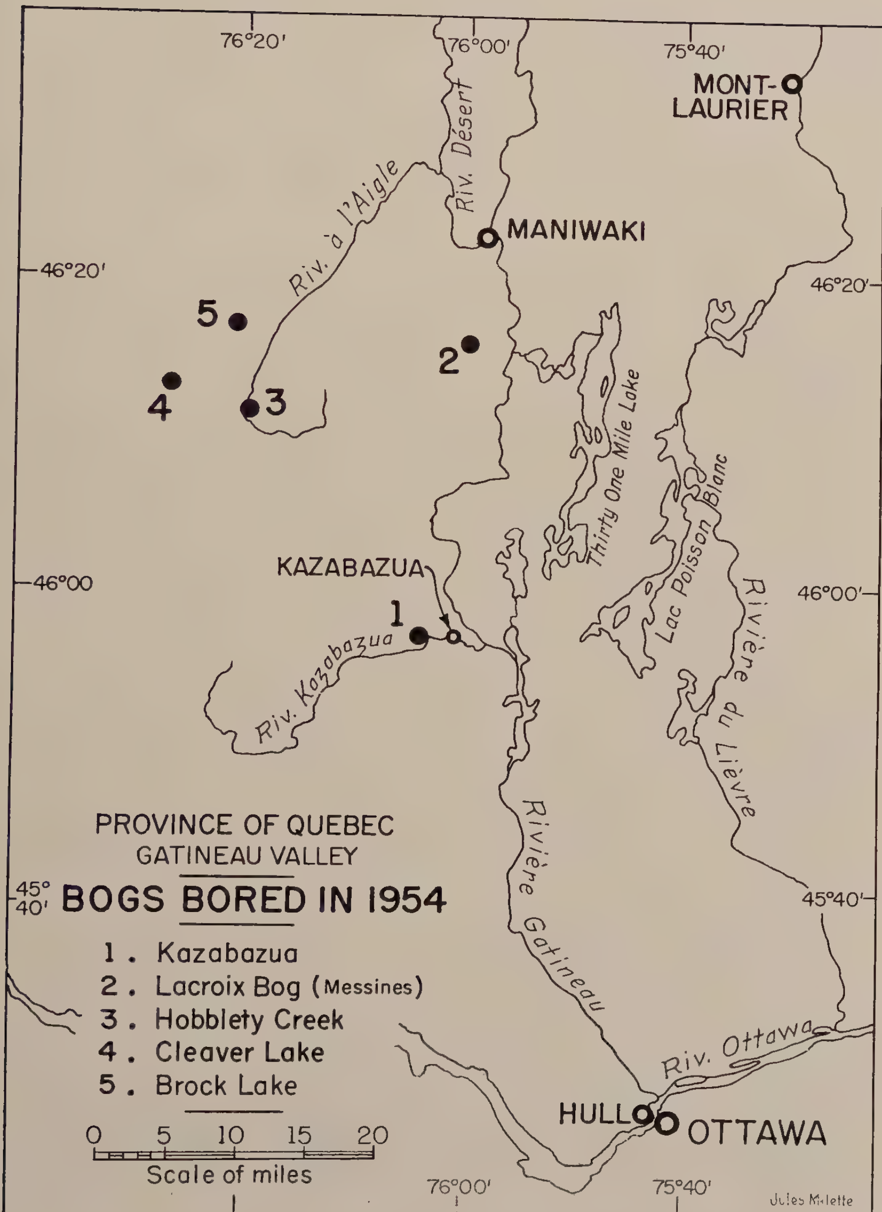

FIGURE 1

Outline map of the Gatineau Valley area and location of Bogs.

Kazabazua Bog (45° 57′ N, 76° 04′ W; alt. about 600 ft.). This is a beautiful deep twin kettle set in glacial moraines. The two basins are separated by a fill wall. While the lower basin still has a central open pool, the upper one (where the boring was made) is completely closed and a dense Sphagnum mat heavily invaded by Chamaedaphne has completely solidified (Fig. 2). The bog is set about twenty feet below the sandy plain. A spruce-tamarack forest covers the separating wall. It is located about one half mile from Kazabazua. The immediate vicinity is cleared land, but forest with pine and oak is not far from the bog.

Lacroix Bog (46° 16′ N, 76° 00′ W; alt. approx. 600 ft.). This bog is located about 9 miles south of Maniwaki along Route No. 3, on the farm (Lot 43) of Mr. Berchmans Lacroix, Messine, Canton Bouchette, Gatineau County. The bog constitutes the deepest central portion of a half mile wide, deep kettle. The northern third of the bog is covered with a sparse spruce-tamarack forest, while the balance of the mat is a dense cover of Ledum and Chamaedaphne. The slopes of the kettle are farmed, but a rocky upland, forming the eastern border, is covered with broad-leaved forest and pine. After several exploratory soundings, the boring was made in the central part of the bog.

Hobblety Creek Bog (46° 11′ N, 76° 21′ W; alt. approx. 700 ft.). This deep-set, small kettle, only about 200 feet across, is completely surrounded by moraines. A small rock basin lake is located only about 50 feet from the bog. Black spruce has invaded the border, and the completely closed surface is a deep mat of Sphagnum. Hobblety Creek bog is 6 miles south of the Eagle Creek Depot along the depot road. Exploratory soundings showed the deepest part of the kettle to be in the central portion.

Cleaver Lake Bog (46° 13′ N, 76° 26′ 35″ W; alt. about 750 ft.) The origin of the bog was apparently a bay or a small lake drained along the eastern border by a creek. The lake was completely filled in, but a recently built dam, a mile upstream from Cleaver Lake, flooded the mat to a depth of two feet. The northeast flanking rocky upland is forested with pine, oak and birch. The low west shore was covered with spruce-tamarack forest. The boring was made in the central part, several hundred feet west of the creek.

Brock Lake Bog (46° 17′ N, 76° 20′ 30″ W; alt. about 700 ft.). The elongate kettle is surrounded by a deep mote, and the mat is in the quaking stage. It is about one mile northwest of the Eagle Creek Depot, a short distance from Brock Lake.

RESULTS

In its gross features, the initial climatic and forest history is strikingly similar to that shown in the bogs of the St. Lawrence valley (5) and northward to Mont Tremblant Park (6). Climate must have been quite warm, for

FIGURE 2

Kazabazua Bog. A typical consolidated kettlehole bog. Covered by a dense mat of Sphagnum, heavily invaded by Chamaedaphne.
J. E. Potzger (right) and Albert Courtemanche.

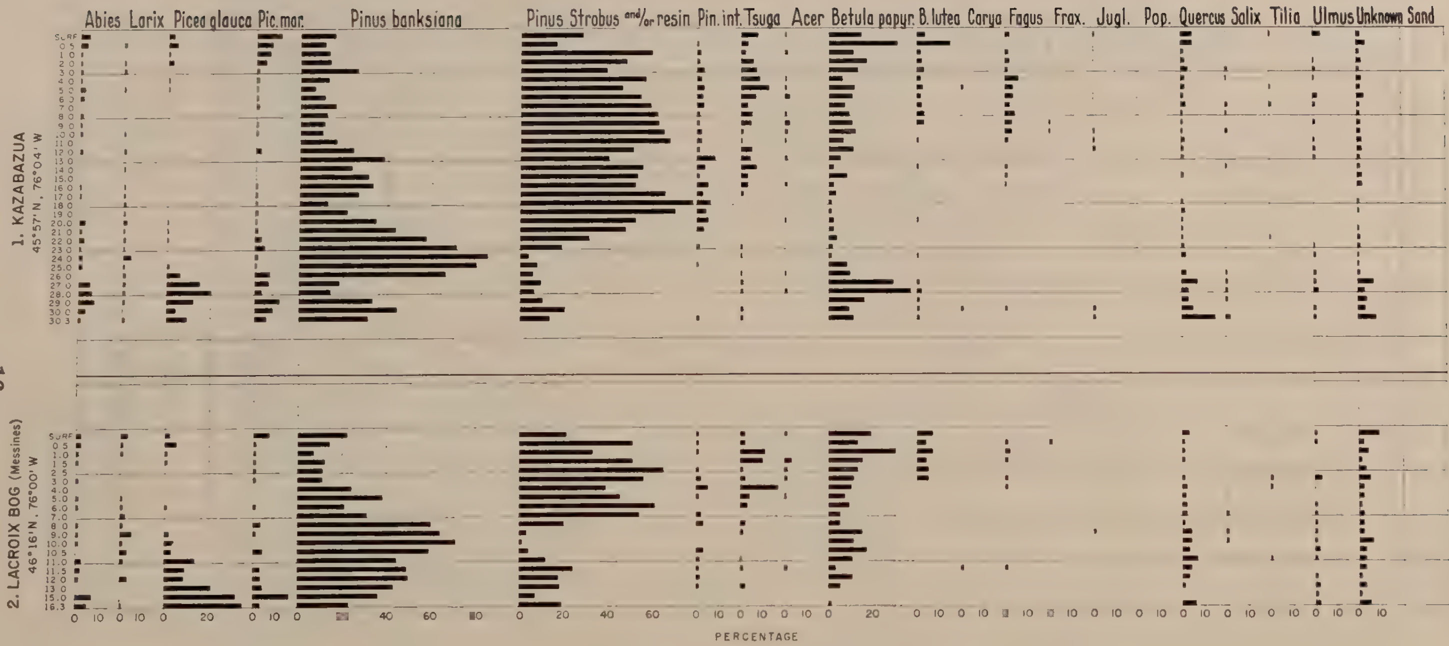

FIGURE 3

Profiles of bogs 1, 2. See text for description.

FIGURE 4

Profiles of bogs 3, 4, 5. See text for descriptions.

TABLE 1

Kazabazua Bog. Numbers of pollen grains of shrubs and herbs tabulated while counting the stated number of three pollens.

		Shrubs							Herbaceous Plants							Pteridophytes					
Foot-levels	No. tree pollens	Alnus	Betula pumila	Cornus	Corylus	Ericaceae	Ilex	Myrica	Lychnis	Gramineae	Carex	Chenopods	Compositae	Nymphaea	Typha	Dryopteris	Osmunda	Lycopodium	Isoetes	Sphagnum	Unknown spores
Surf.	200	4	2	—	2	10	—	—	—	5	—	—	2	—	—	—	—	—	—	54	—
0′6″	150	5	5	—	7	25	—	—	1	18	—	1	14	—	—	—	—	—	—	33	—
1′	200	1	—	—	1	—	—	—	—	1	—	—	1	—	—	—	—	—	—	2	1
2′	"	1	1	—	1	2	—	—	—	1	2	—	—	—	—	—	—	—	—	5	1
3′	150	3	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1
4′	200	—	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
5′	"	1	—	—	—	—	—	—	—	3	3	—	—	—	—	—	—	1	—	1	—
6′	"	—	1	—	1	—	—	—	—	2	1	—	—	—	—	—	—	—	—	13	—
7′	150	1	2	—	—	—	—	—	1	2	3	—	—	—	—	—	—	—	—	7	—
8′	200	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9′	"	1	2	—	—	3	—	—	—	1	2	—	—	—	—	—	—	—	—	1	—
10′	"	3	1	—	—	—	—	—	—	1	2	—	—	2	—	1	—	—	—	—	1
11′	"	3	2	—	—	—	—	—	—	3	1	—	—	1	—	—	—	—	—	1	—
12′	150	2	1	—	1	—	—	—	—	4	—	—	1	—	—	—	—	—	—	—	—
13′	"	3	1	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—	1	—
14′	200	1	1	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
15′	150	5	1	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
16′	200	3	3	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
17′	"	4	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—
18′	"	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
19′	"	2	3	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
20′	"	1	1	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—
21′	"	3	1	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
22′	"	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
23′	"	2	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—
24′	"	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
25′	"	3	—	—	—	—	—	—	—	1	2	—	1	—	—	—	—	—	—	—	—
26′	"	1	—	—	—	1	—	—	—	1	1	—	2	—	—	—	—	—	—	—	—
27′	150	—	3	1	5	2	—	—	—	1	3	—	1	—	—	1	—	—	—	—	—
28′	"	—	4	—	4	—	—	—	—	4	1	—	—	—	—	—	—	—	—	—	—
29′	"	1	7	—	2	—	—	1	—	1	1	—	1	—	2	—	—	—	—	—	15
30′	"	2	8	—	1	—	—	—	—	18	3	—	—	—	3	—	—	—	—	—	64
30′4″	"	—	18	—	—	—	—	—	—	36	11	—	6	—	—	—	—	—	—	—	28

oak had migrated up the valley and showed its greatest abundance in the lowermost levels of all bogs. We have here, as described by Potzger (5) for southern Quebec, climate Q.2, which was much cooler, and spruce developed a prominent peak. After a brief control, it yielded to climate Q.3 or the Jack Pine peak, when spruce and fir declined to insignificance, marking no doubt, the major xerothermic period.

The region differs from the St. Lawrence valley and more easterly stations on the Shield by the persistence of *Pinus strobus-Pinus resinosa* to modern times, marking the region as a "pine belt."

TABLE 2

Lacroix Bog. Numbers of pollen grains of shrubs and herbs tabulated while counting the stated number of tree pollens.

		Shrubs							Herbaceous plants							Pteridophytes					
Foot-levels	**No. tree pollens**	**Alnus**	**Betula pumila**	**Cornus**	**Corylus**	**Ericaceae**	**Ilex**	**Myrica**	**Lychnis**	**Gramineae**	**Carex**	**Chenopods**	**Compositae**	**Nymphaea**	**Typha**	**Dryopteris**	**Osmunda**	**Lycopodium**	**Isoetes**	**Sphagnum**	**Unknown spores**
Surf.	150	8	—	—	4	46	—	—	3	20	—	5	8	—	—	—	—	—	—	1	—
0'6"	"	1	—	—	—	6	—	—	—	3	1	—	1	—	—	—	—	—	—	1	—
1'	"	—	—	—	2	3	—	3	—	—	—	—	1	—	—	—	—	—	—	2	2
1'6"	"	—	—	—	—	1	1	1	—	5	—	—	—	—	—	—	—	—	—	—	1
2'6"	"	1	—	—	—	2	—	—	—	2	—	—	—	—	—	—	—	1	—	10	—
3'	"	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
4'	"	2	3	—	2	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—
5'	200	3	1	—	2	1	—	1	—	—	1	—	—	—	—	—	—	1	—	—	—
6'	150	2	3	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—
7'	"	3	4	—	—	—	—	—	—	1	—	—	1	1	—	—	—	1	—	—	1
8'	"	2	4	—	—	—	—	—	—	2	1	1	—	—	—	—	—	1	—	—	1
9'	"	2	2	—	1	—	—	—	—	3	1	—	2	—	—	—	—	—	—	—	—
10'	"	2	1	—	—	—	—	1	—	11	—	—	—	—	—	—	—	—	—	—	1
10'6"	"	1	3	—	—	—	—	1	—	22	—	—	—	—	—	—	—	1	—	—	1
11'	200	1	4	—	1	—	—	1	—	7	1	—	3	—	—	—	—	—	—	1	1
11'6"	150	—	3	—	—	—	—	—	—	2	—	—	—	—	1	—	—	—	—	—	1
12'	125	2	1	—	1	—	—	—	—	12	1	—	—	—	1	—	—	—	—	—	1
13'	100	—	1	—	1	—	—	—	—	5	—	—	—	—	—	—	—	—	—	—	1
15'	75	—	—	—	—	—	—	—	—	5	—	—	—	—	—	—	—	—	—	—	—
16'4"	100	—	2	—	—	—	—	—	—	2	—	—	2	—	—	—	—	—	—	—	—

The cooler, moist pine-hemlock period is clearly accentuated as well as the later beech-yellow birch interval. This yielded here also, to the second spruce-fir peak. While birch shows a bimodal pattern, correlated somewhat with the cooler spruce-fir period, it does not attain the importance in the forest complex indicated in the Mont Tremblant Park region.

In general, all five types of climate (Q.1-Q.5) expressed in the St. Lawrence valley, are present in the Gatineau valley forest history. The overall climate differed in that it favored white and red pine, and oak was a more prominent pioneer genus than in other parts of Quebec.

DISCUSSION

The Ottawa valley with its tributary, the Gatineau valley, are located mainly within Halliday's (4) forest areas L.4, which he describes as the area where white pine probably reached its maximum development in Canada. To quote him, "Extensive areas within the section originally supported fine stands of white and red pine with a scattering of other species." This description fits very well

TABLE 3

Hobblety Creek Bog. Numbers of pollen grains of shrubs and herbs tabulated while counting the stated number of tree pollens.

		Shrubs							Herbaceous Plants							Pteridophytes					
Foot-levels	No. tree pollens	Alnus	Betula pumila	Cornus	Corylus	Ericaceae	Ilex	Myrica	Lychnis	Gramineae	Carex	Chenopods	Compositae	Nymphaea	Typha	Dryopteris	Osmunda	Lycopodium	Isoetes	Sphagnum	Unknown spores
Surf.	150	3	1	—	6	16	—	1	1	1	—	1	10	—	—	—	—	—	—	3	—
0′6″	"	3	—	—	3	11	—	—	—	—	—	—	2	—	—	—	—	—	—	1	—
1′	"	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2′	"	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3′	"	1	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—
4′	"	—	—	—	1	4	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—
5′	"	—	1	—	1	—	—	—	—	1	1	—	—	—	—	—	—	—	—	1	—
6′	"	2	1	—	—	1	—	—	—	3	2	—	—	—	—	—	—	—	—	—	—
7′	"	—	—	—	1	—	—	—	—	1	—	—	1	—	—	—	—	—	—	1	—
8′	"	2	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—
9′	"	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
10′	"	4	6	—	1	—	—	—	—	2	—	—	—	2	—	—	—	2	—	—	—
11′	"	1	—	—	—	1	—	1	—	1	—	—	2	—	—	1	—	—	—	—	—
12′	"	2	—	—	1	3	—	—	—	—	—	—	—	—	—	—	1	—	—	2	—
13′	200	3	1	—	—	—	—	—	—	—	1	—	2	—	—	—	—	1	—	1	—
14′	150	2	—	—	—	1	—	—	—	—	1	—	—	—	—	—	—	3	—	1	1
15′	200	1	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—
16′	"	—	—	—	1	—	—	—	—	1	—	—	—	1	—	—	—	—	—	2	1
16′6″	150	1	—	—	—	5	—	—	—	3	8	—	—	—	—	—	—	—	—	—	—
17′	"	4	1	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
18′	"	2	1	—	—	1	—	—	—	2	2	—	—	2	—	—	—	—	—	—	—
19′	"	—	1	—	—	—	—	—	—	3	2	—	1	5	1	—	—	—	—	1	—
20′	"	2	2	—	2	—	—	1	—	5	3	—	1	3	1	—	—	—	—	—	3
21′	"	—	1	2	7	1	—	9	—	20	—	1	1	—	—	—	—	1	—	—	12
21′6″	"	—	2	—	2	—	—	5	—	6	1	—	2	—	—	—	—	—	—	—	15
21′3″	85	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1

the records of the pollen profiles from the five bogs of that region. The five pollen profiles also correlate favorably with those reported by Potzger and Courtemanche (7) from Newington, Alfred and St. Lin bogs. According to pollen records, this pine belt once extended much farther into the Laurentian upland, with significant abundance to Lat. 48°. On the Shield, the pine dominance was depressed to insignificance at the close of the major xerothermic period, but not in the Gatineau valley region. There is a decrease of pine in the topmost half-foot of the peat, but this might well represent the disturbance by man, as described by Halliday (4). By observation, it is very plain that the region is still pine country, and splendid stands of pine are rebuilding by secondary succession.

Here, as in all of lower Quebec, Jack pine replaced the spruce-fir period. This Jack pine dominance swept across Quebec to its present outpost at Lat. 49°

TABLE 4

Cleaver Lake Bog. Numbers of pollen grains of shrubs and herbs tabulated while counting the stated number of tree pollens.

		Shrubs							**Herbaceous plants**							**Pteridophytes**					
Foot levels	**No. tree pollens**	**Alnus**	**Betula pumila**	**Cornus**	**Corylus**	**Ericaceae**	**Ilex**	**Myrica**	**Lychnis**	**Gramineae**	**Carex**	**Chenopods**	**Compositae**	**Nymphaea**	**Typha**	**Dryopteris**	**Osmunda**	**Lycopodium**	**Isoetes**	**Sphagnum**	**Unknown spores**
Surf.																					
2′3″	150	4	2	—	2	2	—	—	—	18	—	—	5	—	—	—	1	—	—	11	1
3′	200	1	—	1	8	2	—	2	—	13	3	—	—	—	—	—	—	—	—	3	3
4′	"	2	—	—	—	4	—	3	—	8	1	—	—	—	—	—	—	—	—	1	1
5′	150	1	—	1	1	1	—	1	—	2	7	—	—	—	—	—	—	—	—	8	—
6′	"	2	—	—	3	3	—	1	—	5	1	—	—	—	—	—	—	—	—	7	—
7′	200	1	1	—	3	—	—	2	—	4	1	—	—	—	1	—	—	—	—	1	1
8′	"	—	—	—	1	2	—	—	—	2	1	—	—	—	—	—	—	—	—	1	—
9′	"	2	—	—	1	1	—	—	—	2	1	—	—	—	—	—	—	—	—	—	—
10′	"	6	1	—	1	—	—	—	—	—	2	—	—	2	—	1	—	—	—	—	—
11′	150	3	—	—	—	—	—	—	—	1	—	—	1	3	—	—	—	—	—	—	1
12′	200	7	1	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—	1
13′	"	1	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—
13′6″	"	8	1	—	1	1	—	—	—	7	1	—	1	—	—	—	—	—	—	—	—
14′	"	4	—	—	—	—	—	—	—	2	2	—	1	—	—	1	—	—	—	—	—
15′	"	1	7	—	1	—	—	—	—	4	—	—	1	—	2	—	—	—	—	—	—
15′6″	"	1	4	—	1	—	—	—	—	1	2	—	—	1	—	—	—	1	—	—	1
16′	150	2	8	—	6	—	—	4	—	2	4	—	—	—	1	—	—	—	—	—	1
16′6″	"	—	1	—	1	1	—	—	—	4	1	—	—	—	—	—	—	—	—	—	—
17′	"	3	5	—	5	1	—	3	—	7	1	—	—	—	1	—	—	—	—	—	1

to 50°. Flight over this belt impresses one with the controlling part this lowly pine plays in the forests at these latitudes. Potzger and Courtemanche (7) found that following the major xerothermic period with subsequent cooling, Jack pine pressed southward to replace the crowding white and red pine forests, which is shown in the profiles as a bimodal peak in bogs from Clova (Lat. 48° N) northward. This "revival" of dominance faded to an "echo" at Lat. 46° of the Gatineau valley. The recent cool period is recorded however, even at Lat. 46°, by the weak recovery of spruce and fir (Figs. 3, 4).

One can hardly overlook the early prominence of oak in these Gatineau valley profiles. Unfortunately pollen studies do not well permit ascertaining if one or all species of oak present in the Gatineau valley today were involved. If the pioneers migrated northward, they soon fanned out eastward to the Laurentian upland in the Mont Tremblant region, where they are at present, less abundant in number than in the Gatineau valley. Only one species of oak, *Quercus rubra,* is found in relic groups in the Mt. Tremblant Park area.

The five climatic changes and fluctuations (Q.1 to Q.5) listed by Potzger (5) and Potzger and Courtemanche (7) for southern Quebec and the St.

TABLE 5

Brock Lake Bog. Numbers of pollen grains of shrubs and herbs tabulated while counting the stated number of tree pollens.

		Shrubs							Herbaceous plants							Pteridophytes					
Foot-levels	No. tree pollens	Alnus	Betula pumila	Cornus	Corylus	Ericaceae	Ilex	Myrica	Lychnis	Gramineae	Carex	Chenopods	Compositae	Nymphaea	Typha	Dryopteris	Osmunda	Lycopodium	Isoetes	Sphagnum	Unknown spores
Surf.	200	3	—	—	1	6	—	—	—	5	1	2	10	—	—	—	—	1	—	8	—
2′6″	"	—	1	—	3	1	—	—	—	1	1	—	—	—	—	1	—	—	—	—	—
3′	150	1	—	—	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—
4′	200	3	—	—	3	2	2	—	—	3	—	—	1	—	—	—	—	—	—	—	—
5′	"	2	—	—	2	4	2	—	—	2	—	—	—	—	—	1	—	1	—	1	—
6′	"	2	1	—	—	1	1	—	—	3	—	—	—	—	—	—	—	—	—	12	—
7′	"	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8′	150	4	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9′	"	7	1	—	1	1	—	—	—	6	—	1	1	—	—	—	—	—	—	—	3
10′	"	2	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
11′6″	"	3	—	—	1	—	—	—	—	2	4	—	—	2	—	—	—	—	—	—	—
12′	200	—	1	—	—	—	—	—	—	4	6	—	—	—	—	—	—	—	—	—	10
12′6″	"	—	5	—	—	1	—	—	—	5	4	—	2	—	—	—	—	1	—	—	20
13′	"	—	6	—	1	3	—	—	—	8	2	—	1	1	—	—	—	—	—	—	59

Lawrence valley also left their imprint on the forest history of the Gatineau valley. When one compares the profiles with those reported by Potzger and Courtemanche (6) from lakes and bogs of the Mont Tremblant area, some differences stand out. Spruce and fir are less abundant, the hemlock peak has only half the prominence it indicates in the Mt. Tremblant area as far north as Lac Monroe, and progressive decline of white and red pine is not apparent. When the native vegetation comes under the influence of civilized man, it is difficult to separate climatic control from physiographic influences. However, in the Mont Tremblant region, undisturbed secondary succession after lumbering shows lack of reproduction by pine, suggesting continuence of climatic factors which began to militate against pine long before civilized man entered the picture. The excellent reproduction by pine observed in the Eagle Creek area suggests that pine here is still climatically favored. Halliday (4), however, says, "In spite of the previous dominance of these species (white and red pine) and the presence of intrusive conifers from the Boreal Forest region, the general characteristic is that of a mixed forest, and the dominant or competitive association is one of sugar maple, yellow birch, hemlock and white pine." Unfortunately sugar maple is so underrepresented in pollen profiles that no conclusion can be drawn about its importance in the forest cover. As stated above, the profiles suggest a climate favorable to pine. There is no doubt that pine tends to be over-emphasized in pollen profiles, but not to the extent that it would be elevated from a minor to a major position. Particular reference is here made to

the profiles from the Mont Tremblant area (6). The decline of pine at the 6 inch level in the Gatineau valley profiles is interpreted as representing the influence of civilized man.

SUMMARY

Pollen frequencies in the deposits of five bogs covering a radius of about 50 miles in the Gatineau Valley of Quebec were determined by conventional methods of pollen analysis. It is concluded that the Gatineau Valley was one of the most important routes for plant migration during early post-glacial times. An initial warm period (similar to that of all southern Quebec) is suggested by highest abundance of oak in the first or second foot-level and pine forest cover with very low spruce fir. Cooling climate followed soon, marked by a decided increase in abundance of spruce. Succession is similar at all five bogs. Pine (low oak peak) to pine-spruce, to Jack pine, while spruce and fir decreased to negligible representation, to white-red pine with minor hemlock peak, to pine-spruce-fir-birch which suggests cooling climate during the recent past. The Gatineau valley apparently differs climatically from all of southern Quebec and the Mont Tremblant Park region, which can not be attributed to latitude alone.

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POLLEN FROM MOSS POLSTERS ON THE MAT OF LAC SHAW BOG, QUEBEC, CORRELATED WITH A FOREST SURVEY

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Pollen analysts have always been haunted by the uncertainty of pollen representation proportionate to the forest complex they were to represent, and comparatively little work has been done on this important problem. Caroll (3) investigated the problem in the Great Smoky Mountain area, Hansen (4) in a western forest region, and Cain (1) in 1953 began an extensive piece of work covering a wide geographical area. His plan was to associate moss polster pollen representation with basal area of trees in 1/10 to two acre plots. The present writers felt that such an approach does not well harmonize with the modus operandi in nature, when pollen settles out on the open surface of a lake or on a bog mat. They further felt that most of the plots (1/10 acre) were too small a unit on which to base the composite pollen rain of a given region, especially when the aim is to determine the over- and under-representation of certain genera. So it was planned to select a natural situation, i.e., an open bog mat and a more extensive analysis of the bordering forest, and to associate with such quadrat study pollen percentages obtained from moss polsters. The small Lac Shaw bog, one and a half miles south of the Mont Tremblant Biological Station, seemed ideally suited to such a study (Fig. 1), especially since Potzger and Courtemanche (7) had already presented a pollen profile from this bog.

The surrounding forest is a typical spruce-fir *(Picea-Abies)* forest of a lowland habitat which was in late secondary succession after selective cutting. The association consists primarily of coniferous species, but a prominent rocky upland a half mile north and northwest of the bog is covered with a dense broadleaved forest primarily paper birch *(Betula papyrifera)*, yellow birch

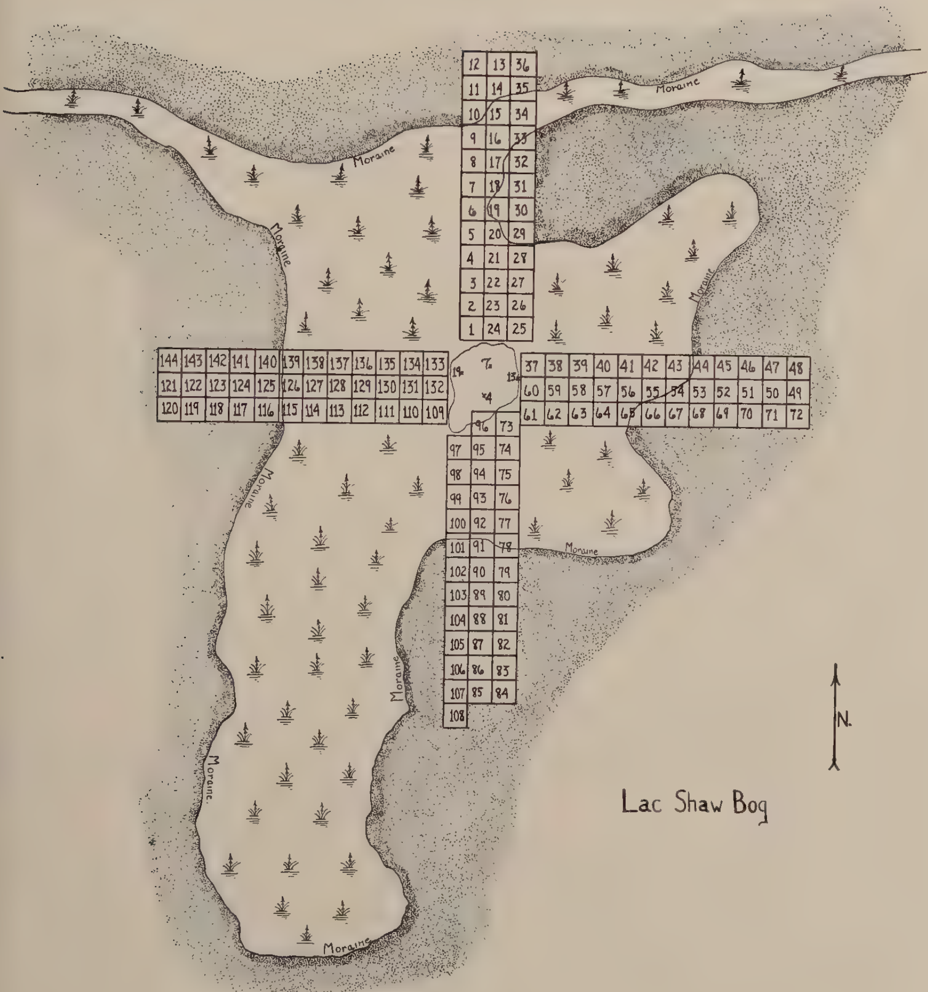

FIGURE 1

Map of the Lac Shaw Bog and surrounding territory, showing the location of moss polster samples on the open mat at the center, and the 144 forest quadrats in the adjacent area.

(Betula lutea) and sugar maple *(Acer saccharum)*. The lowland forest is "belted," determined in this characteristic by a low surrounding moraine (Fig. 1), and the completely closed former bog mat, which is covered by a dense coniferous forest except for the 200 x 200 foot open central area. The whole mat is still quite wet.

METHODS

In order to obtain a record of the sociology of the border forest, the quadrat method was used to obtain data on per cent F. I. (frequency index), density, size classes and reproduction. The unit was a 10 x 10 meter quadrat. Four lines of quadrats were laid out as three rows of 12 quadrats each (Fig. 1) radiating from the bog's open central area along the four main directions (N, E, S, W). The 144 quadrats total approximately 3.6 acres. Lines were run by compass direction. In order to facilitate both laying out of quadrats as well as tabulating, stakes were driven at each corner of the quadrats and the areas were then delimited by white string. This system also made possible the numbering of each quadrat (Fig. 1) and associating moss polster collections with definitely numbered quadrats. The diameter at breast height (D. B. H.) of trees was measured with wooden calipers. All stems below one inch D. B. H. but at least three feet in height were tabulated to record established reproduction of the various associates. Moss polsters were taken at a number of points on the mat (Fig. 1) and in quadrats of the forest survey. Shrubs were listed only for presence in a quadrat. Basal area was calculated for the various tree species.

In the laboratory, parts of the moss polsters were stirred vigorously in hot 95% alcohol, strained through cheesecloth to remove coarse particles, and the finer particles, constituting the sediment in the beaker, were stained with gentian violet. Glycerine jelly served as mounting medium. Tabulation followed customary procedures in pollen analysis. While pollen rain associated with bordering forest was the main aim of the study, detailed sociological analysis of a Quebec spruce-fir forest in secondary succession is included in the work. Cain (2) has pointed out that red spruce *(Picea rubens)* is frequently an important element in the Mont Tremblant Park forests, but since it is not easy to differentiate between black *(Picea mariana)* and red spruce in the field, especially when trees are young, and since pollens of red spruce closely resemble those of white spruce *(Picea glauca)*, no differentiation was attempted in the pollen counts between white and red spruce.

Comparisons of pollen percentages are correlated with stems 6-inches or above in diameter (Fig. 2) because such stem-size individuals would very likely participate in pollen production.

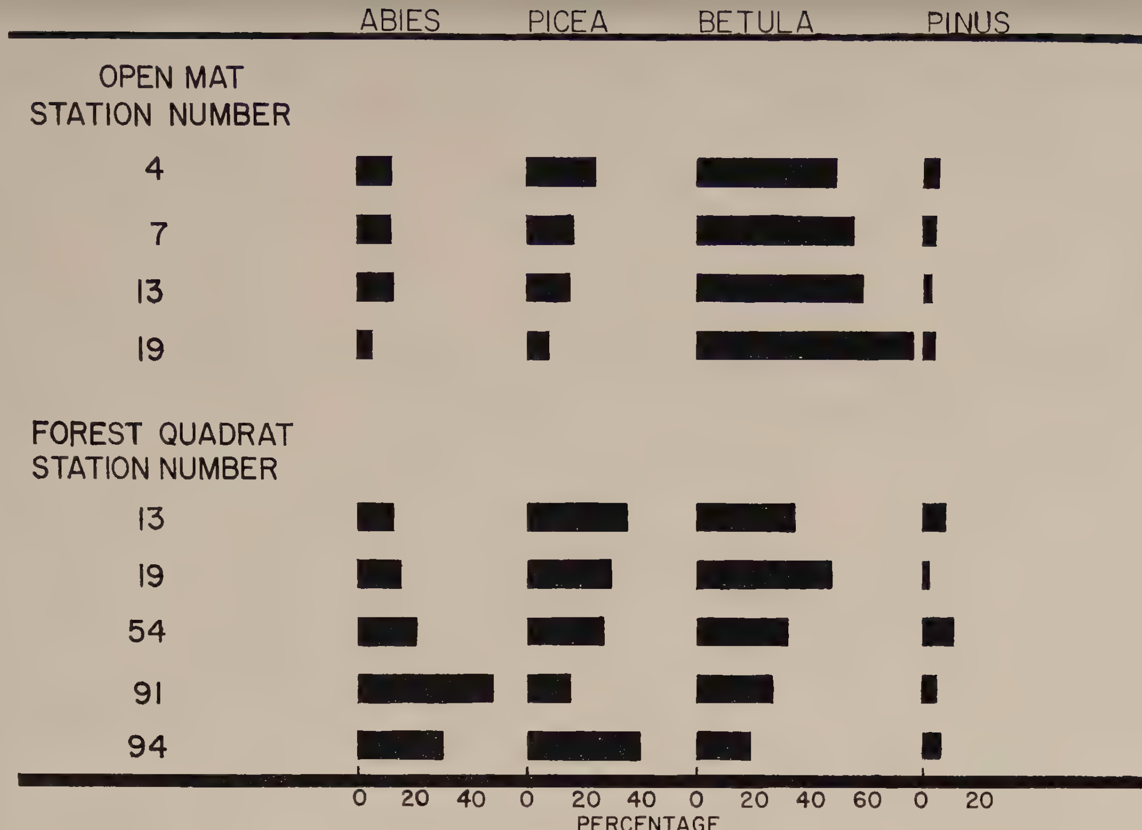

FIGURE 2

Pollen frequencies of four genera from four moss polster samples obtained from the open mat, in comparison with pollen frequencies from moss polsters from five selected stations in the adjacent forest. See figure 1 for locations of stations.

RESULTS

Forest Survey

Table 1 presents the results of the quadrat study in summary form. From the per cent F. I. and density (abundance) we may classify the forest as spruce-fir in which birch and arbor vitae *(Thuja)* play an important role. Arbor vitae is limited chiefly to the west and north sectors. Birch is limited to the low morainic borders. Fir *(Abies)* surpasses all species in reproduction, and since foresters are very much interested in reproduction ratios between spruce and fir, it may be noted that at this station the ratio is about 3:1 in favor of fir. Thuja displays a vigorous reproduction but *Larix* shows no aggressive participation in the reproduction nor in the crown control, not a single stem above 1-inch D. B. H. appearing in the survey. *Acer saccharum* (sugar maple) is limited to the moraines in its invasion, but at present it promises no aggressive competition. Of the tall shrubs or small trees, *Pyrus americana* (Mountain ash) and *Acer spicatum* (Mountain maple) are most abundant, the latter usually growing in dense clumps as result of root sprouting. Abundance is high but per cent F. I. is only 48%.

Stems of all species which are 3 inches in diameter or above total 1982, or 550 stems per acre. Such great abundance is indicative of successional status, in this case secondary succession. Basal area in sq. ft. per acre listed in order of decreasing amounts for most important species is as follows:

Thuja	34.060
Abies	29.844
Picea mariana	25.695
Betula lutea	11.640
Picea rubens	3.747
Betula papyrifera	1.876
Picea glauca	.891
Acer rubrum	.353

Of the shrubs only *Nemopanthus mucronata* has a wide distribution (F. I. 56) and of the small trees *Acer spicatum* (F. I. 48). Total number of shrub species is high (19).

MOSS POLSTER STUDY

Summary results are shown in figure 2, and abundance of stems used for comparison with pollen percentages are shown in tables 1 and 2. Outstanding, easily recognizable differences in the pollen percentages are extreme under-representation of *Thuja, Larix, Acer* and all shrubs, including such common mat species as *Chamaedaphne* (Leatherleaf) and *Kalmia*, as well as the widely

TABLE 1

Size classes in inches D. B. H. and Basal Area, and percent Frequency Index, of trees and shrubs in a total of 144 quadrats, each 100 square meters in size. See figure 1 for location of quadrats.

Species	Below 1 in.	1	2	3-5	6-9	10-15	16-20	Above 20	Total	% F. I.	Basal area sq. ft. per acre
Abies balsamea	964	631	611	746	160	4	—	—	3116	90.0	29.844
Acer rubrum	45	4	2	2	5	—	—	—	58	24.0	0.353
A. saccharum	10	—	1	—	—	—	—	—	11	4.0	—
Betula lutea	13	20	22	45	29	13	1	2	145	42.0	11.640
B. papyrifera	8	17	38	46	7	1	—	—	117	34.0	1.876
Fraxinus nigra	—	—	—	1	—	—	—	—	1	0.7	0.024
Larix laricina	97	5	—	—	—	—	—	—	102	9.0	0.006
Picea glauca	—	—	3	4	6	—	—	—	13	5.5	0.891
P. mariana	392	245	215	377	173	10	—	—	1412	78.0	25.695
P. rubens	2	—	—	6	8	6	—	—	22	7.0	3.747
Pinus strobus	—	—	—	1	—	—	—	—	1	0.7	0.014
Prunus pennsylvanica	21	2	2	1	—	—	—	—	26	13.0	—
P. serotina	—	1	1	5	—	—	—	—	7	2.7	—
Salix	4	—	—	—	—	—	—	—	4	0.7	—
Thuja occidentalis	278	94	61	110	73	37	3	1	657	29.8	34.060
SMALL TREES AND SHRUBS											
Acer spicatum	1037	21	—	—	—	—	—	—	1058	48.0	—
Pyrus americana	102	2	—	—	—	—	—	—	104	28.0	0.086
Alnus rugosa	—	—	—	—	—	—	—	—	—	26.0	—
Amelanchier	—	—	—	—	—	—	—	—	—	2.7	—
Chamaedaphne	—	—	—	—	—	—	—	—	—	5.5	—
Corylus cornuta	—	—	—	—	—	—	—	—	—	13.0	—
Diervilla lonicera	—	—	—	—	—	—	—	—	—	6.2	—
Kalmia	—	—	—	—	—	—	—	—	—	25.7	—
Ledum groenlandicum	—	—	—	—	—	—	—	—	—	1.4	—
Lonicera	—	—	—	—	—	—	—	—	—	2.7	—
Myrica gale	—	—	—	—	—	—	—	—	—	7.5	—
Nemopanthus mucronata	—	—	—	—	—	—	—	—	—	56.0	—
Ribes	—	—	—	—	—	—	—	—	—	2.0	—
Rubus	—	—	—	—	—	—	—	—	—	2.7	—
Sambucus	—	—	—	—	—	—	—	—	—	5.5	—
Spiraea latifolia	—	—	—	—	—	—	—	—	—	2.7	—
Vaccinium	—	—	—	—	—	—	—	—	—	33.3	—
Viburnum alnifolia	—	—	—	—	—	—	—	—	—	31.8	—
Viburnum cassinoides	—	—	—	—	—	—	—	—	—	31.9	—

TABLE 2

Percentages of pollen in moss polster samples from both open mat and selected forest stations. See figure 1 for locations of stations.

Species	Open Mat Stations					Forest Quadrat Stations					
	4	7	12	19	Average of 4 Stations	13	19	54	91	94	Average of 5 Stations
Abies	12.0	12.0	12.5	5.0	10.5	0.5	—	0.5	—	—	0.2
Larix	0.5	—	2.0	0.5	1.0	16.0	4.5	6.0	1.5	12.5	8.1
Picea glauca	5.0	5.0	6.0	4.0	5.0	19.5	25.5	21.0	14.0	27.5	21.5
Picea mariana	19.5	11.5	9.0	3.5	10.5	5.5	1.5	4.5	2.5	2.5	3.3
Pinus banksiana	1.5	1.5	1.0	2.0	1.5	2.5	0.5	6.0	2.5	4.0	3.1
Pinus strobus	4.0	3.0	2.0	2.0	3.0	0.5	0.5	0.5	—	—	0.3
Pine (intermediate)	—	—	—	—	—	0.5	0.5	1.5	—	1.0	0.7
Tsuga	1.0	1.5	1.0	1.0	1.0	—	—	—	—	—	—
Thuja	1.5	1.5	—	0.5	1.0	1.0	—	—	1.0	—	0.4
Acer	1.5	2.0	0.5	2.0	1.5	11.0	12.0	14.5	10.0	5.5	10.6
Betula papyrifera	15.0	27.0	22.5	28.5	23.3	24.0	36.0	18.0	17.0	13.5	21.7
Betula lutea	34.5	28.5	36.5	48.0	37.0	0.5	—	—	—	—	0.1
Fagus	—	—	1.0	—	—	—	—	—	—	—	—
Fraxinus	—	0.5	—	—	—	—	—	—	—	—	—
Populus	—	—	1.0	—	—	—	0.5	0.5	0.5	0.5	0.4
Quercus	1.0	1.0	0.5	0.5	1.0	—	—	—	—	—	—
Salix	—	—	—	0.5	—	0.5	0.5	1.0	1.0	—	0.6
Ulmus	0.5	1.5	0.5	0.5	1.0	1.0	4.0	3.0	—	—	1.6
Alnus	—	1.0	1.0	3.0	—	—	—	—	2.0	—	0.4
Betula pumila	—	—	—	1.0	—	—	—	7.0	1.0	4.0	2.4
Corylus	—	1.0	—	—	—	8.0	—	—	—	—	1.6
Ericaceae	—	—	—	—	—	2.0	5.0	4.0	3.0	1.0	3.0
Myrica	22.0	8.0	—	12.0	—	6.0	1.0	18.0	1.0	1.0	5.4
Gramineae	10.0	2.0	9.0	6.0	—	—	—	1.0	—	—	0.2
Carex	—	—	—	—	—	—	—	2.0	—	—	0.4
Chenopods	1.0	—	2.0	—	—	8.0	9.0	14.0	3.0	4.0	7.6
Compositae	10.0	9.0	12.0	8.0	—	1.0	—	—	—	—	0.2
Typha	—	—	—	—	—	—	—	—	—	—	—
Lycopodium	2.0	1.0	—	1.0	—	5.0	2.5	4.5	1.5	3.0	3.3
Unknown	2.5	3.5	4.0	1.5	3.0	13.0	15.5	21.0	48.0	30.0	25.5

distributed *Nemopanthus*. It is very likely that *Nemopanthus, Alnus, Corylus* and *Spiraea* produce none or very few flowers in the shade of the forest where most of them were observed. The most over-represented genus in polsters from the bog mat is *Betula*. Apparently over-represented to a lesser degree is pine, while fir is under-represented. Closest correlation between pollen and forest representation is in spruce *(Picea)*.

It is quite obvious that moss polsters taken in quads located in a forest stand show the influence of pollen rain of trees within that area, and so will not represent a regional forest condition. It is also apparent that a wide area participates in the pollen rain falling on an open area, such as a lake or a bog mat. The high percentage of birch pollen from polsters on the mat suggests that the birch forest a half mile north and west of the bog contributes much of the birch pollen settling out on the mat. Pine has a very sparse representation in the border forest but shows a five percent representation in the pollen record. This too points to longer distance transfer. The nearest station for jack pine *(Pinus banksiana)* is perhaps 15 miles to the northwest.

Tree genera not present in the forest survey but appearing in the pollen record of the moss polsters (Table 2), and known as minor elements in nearby forests are: *Ulmus, Tsuga, Acer, Fagus, Fraxinus, Populus*. Trees appearing in the pollen record (Table 2) which have not been reported from nearby areas, but are known to be present in forest stands 5 to 15 miles distant are *Quercus* and *Pinus banksiana*.

DISCUSSION

Forest Survey

The forest of the Mont Tremblant Park area is difficult to fit into a definite pattern because of the unusual characteristics in the distribution of the various species. At times one wonders if there is any pattern involved. Frequently there is also a baffling association of species. Tops of mountains may be covered by spruce-fir or yellow birch, or sugar maple, beech and yellow birch with intrusion of hemlock. Elsewhere spruce-fir may form dense stands in valleys. While white pine is at present a relic in spruce-fir as well as in broadleaved forests, it may at times appear in considerable abundance, as on the slopes above Lac des Femmes (adjacent to the Biological Station).

The border forest around Lac Shaw bog is more definitely a spruce-fir type in which arbor vitae and birch play a considerable part. At the Lac Savanne bog in the same general region, which we may use for comparison, the forest is nearly all spruce-fir. If one were to estimate from general observation the species which have greatest abundance in the Lac Monroe area (which includes the Lac Shaw bog station) one would say without hesitation yellow birch

(formerly no doubt white birch in addition to yellow birch). The Lac Shaw forest as presented in Table 1 leaves no doubt of its classification as spruce-fir type. In spite of former cutting we find in the 3.6 acre survey 203 stems (chiefly black spruce) and 164 stems of fir 6 inches or above in diameter. Reproduction is high, on an average 271 small trees up to three inches D.B.H., plus 175 saplings of 1-inch D.B.H. per acre.

Foresters are of course interested in the spruce-fir ratio. Here as in many or most other localities of the region, fir is reproducing more abundantly than spruce. At Lac Shaw bog one finds abundant decaying logs, so that the difference in reproduction is not, as sometimes assumed, due to lack of organic material to favor reproduction of spruce. Since fir is also more shade tolerant than spruce, the end of succession in the Lac Shaw bog forest may, indeed, give fir importance in the forest cover.

It is very interesting to note how similar the dominants in the Laurentian Shield stand are with respect to density, frequency, reproduction and even in associated species to spruce-fir stands elsewhere—those in Great Smokies as reported by Oosting and Billings (5) and especially to stands in the White Mountains of New Hampshire as reported by the same authors. The dominant genera spruce and fir also show great similarity in their sociology to the spruce fir forest of the Medicine Mountains, Wyoming, as described by Oosting and Reed (6).

The Canadian stand differs from the other spruce-fir stands referred to in that three species of spruce enter into the forest complex. Greatest similarity is to the New Hampshire stands. This would be expected because of the greater similarity in geographical location. However the Laurentian stand has double the number of associated tree species and a larger number of shrubs associated with it. This may be due to the greater number of quadrats included in the Canadian study, or to habitat differences, or also to successional influences. For more comparable results one should no doubt select an upland rather than a lowland spruce-fir stand in the Mont Tremblant region.

As refererd to previously, the dominants are strikingly similar in their phyto-sociological expression in all the spruce-fir stands mentioned. The greater abundance of *Abies* may be due to climatic control, for at latitudes north of Mont Tremblant Park spruce surpasses fir in abundance.

Moss Polsters

It seems quite certain that moss polster studies will hardly be a solution to the problems involved in absolute correlation of pollen percentages and abundance of genera and species constituting the forest composition. The present study emphasizes, however, that among the factors which enter into the prob-

lem of pollen representation are local and regional participation in the pollen rain and interferences with the settling out process as such. The results of this study strongly indicate that a coniferous forest interferes with deposition of pollen in moss polsters beneath its crown. We should point out some confidence-inspiring features of this moss polster study. Field workers in the Mont Tremblant Park forests would be much disappointed if such infrequent genera as *Ulmus, Tsuga, Fagus, Fraxinus* and *Acer* did not appear in a moss polster pollen record in the park. They are rare elements in these forests but one need not necessarily search for them. Their appearance in the pollen records makes the forest community read into a pollen profile more real.

If one does not expect to find an absolute mathematical correlation between numbers of stems and pollen percentages, the over-all characteristics of the forest are fairly well pictured, but we must not assume that the pollen profile represents only a limited bordering area. After several years of field work in this region one would be disappointed if *Quercus* and jack pine had not appeared in the pollen record. If the pollen rain settles out on a body of water, over-representation of a bordering forest is also modified. This is indicated by the pollen profile of upper inches from the sediments in Lac aux Atocas as shown by Potzger and Courtemanche (7).

It is no doubt necessary to assume a regional participation in the pollen rain, especially in an open location such as a lake or an open bog mat. Even on a bog mat the central position (See 4, 7 on Table 2) appears to record more uniformly the same percentages for the various genera. One should, therefore, use more than one moss polster sample and average the percentages. There is no doubt that moss polsters taken beneath the forest canopy reflect to some extent very narrow local influences. This is especially emphasized by quadrat 91 where *Abies* has an unusual high pollen representation (Fig. 2) and also a high total abundance of stems. *Betula* as a whole has a much lower representation in stations located within the forest. This may be due to interception of the pollen rain by the dense crowns of the conifers. If one disregards *Thuja,* the pollen percentages emphasize the three most important components of the forest, provided one does not delimit the area to be represented too much.

The inadequate representation of such shrubs as *Nemopanthus, Alnus, Kalmia, Chamaedaphne* and other Ericads is perhaps not a serious problem in forested regions, but it is a disconcerting defect in tundra areas where shrubs become diagnostic and constitute the tallest vegetation.

SUMMARY AND CONCLUSIONS

1. The study presents a 3.6 acre quadrat survey (144 ten by ten meter quadrats) of a spruce-fir forest adjacent to Lac Shaw bog in Mont Tremblant

Park. Associated with the forest survey was a pollen representation in moss polsters to determine reliability of pollen percentages to indicate forest composition.

2. The forest is predominantly spruce-fir with strong participation of arbor vitae and birch in the forest community. While both birch and black spruce have abundant reproduction, fir dominates spruce by three to one.

3. In the pollen records arbor vitae, tamarack, *Acer spicatum* and all shrubs are poorly represented.

4. Pine and birch are over-represented, especially on the bog mat, if only the bordering forest is considered. High representation of birch probably reflects the dense birch forest on uplands a half mile west and north of the bog.

5. Collections of polsters under the forest cover show great variation in pollen representation of the various genera. This is attributed to the influence of nearby trees.

6. Pollen percentages from moss polsters taken on the mat do not reflect the forest of the first thirty meters encircling the bog. This rules out the assumption that pollen rain over a lake or a bog is contributed chiefly by trees nearest the basin.

7. Dense crown cover of a coniferous forest seems to interfere with settling out of birch pollen from outside areas.

8. From a superficial evaluation of the forest composition of the whole region the pollen record from the bog mat polsters presents a more representative picture than any of the collections made under forest cover.

9. Results of the study will not permit assigning "values" to a given genus on the basis of which to estimate over- and under-representation of the associates which appear in a pollen profile, especially if polster collections are made under the forest cover. Even a 3.6 acre survey of a forest adjacent to a bog is inadequate as a basis upon which to correlate mathematically the abundance of certain genera and species with their representation in a pollen rain.

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THE CHARACEAE OF NEBRASKA—ADDITIONS AND CHANGES

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Since the joint studies by Kiener (4) and Daily (1) on the Characeae of Nebraska in 1944, numerous collections have been made in the state. They are reported here with some changes in nomenclature in the interest of consistency or priority as presently conceived, descriptions, illustrations and a complete key. All collections cited in this report were made by Walter Kiener except one. The first set of specimens is in the herbarium of Fay Kenoyer Daily, the second set is in the herbarium of the University of Nebraska, and successive sets are in various other herbaria.

In 1944, Kiener (4) reported on 141 collections made in 36 counties. Together with this paper 357 collections are now reported. Thus 216 collections were added. The area of collection was extended over seven more counties, making a total of 43 counties. This number is slightly less than half of the 93 counties in Nebraska. Some aquatic habitats in every county have been examined at some time or other without finding any Characeae. Yet, a specific search will eventually reveal some in nearly all counties, although some counties do not appear to have suitable habitats for these plants.

In the last few years, Nebraska has again entered a cycle of somewhat less rainfall which in turn reduces the number of rainwater basins as well as the seasonal duration during which water remains standing. Inasmuch as the species of Nitella in Nebraska are largely restricted to these basins, the chances of their occurrence were very slim.

The sandhill area, comprising about 20,000 square miles, with many marshes and shallow lakes has not yet been explored. From preliminary sampling, however, it appears that species of Characeae are important members of the plant populations in these lakes and marshes and eventually may reveal interesting plant-life stories.

We wish to acknowledge the cooperation of W. A. Daily, the late J. E. Potzger and John E. Pelton of Butler University, Francis Drouet of Chicago Natural History Museum, and D. P. Rogers of New York Botanical Garden.

KEY TO THE CHARACEAE OF NEBRASKA

Coronula of two superimposed rows of five cells each.

Antheridia terminal; mature oospore laterally compressed............NITELLA

Ultimate rays of branchlets one-celled; coronula deciduous.

Monoecious.

Heterophyllous (branchlets of two sorts; accessory, simple branchlets produced below and alternately with once-furcate branchlets)..1. *Nitella clavata*

Homoeophyllous (branchlets similar, once-furcate)

Ultimate rays acuminate..................................2. *N. acuminata*

Ultimate rays acute..3. *N. flexilis*

Dioecious; branchlets simple, once-furcate........................4. *N. opaca*

Ultimate rays of branchlets two-celled; coronula persistent.

Fertile branchlets contracted into axillary heads............5. *N. axillaris*

Fertile and sterile branchlets similar.

Plant small; ultimate rays long (½ length of branchlet)...6. *N. confervacea*

Plant large, ultimate rays variable with some very short...7. *N. oligospira*

Antheridia lateral; mature oospore terete..............................TOLYPELLA

Sterile branchlets divided; coronula persistent........8. *Tolypella intricata*

Sterile branchlets undivided.

Lateral and ultimate rays considerably attenuated; coronula persistent; outer membrane of oospore not decorated....9. *T. prolifera*

Lateral and ultimate rays not much attenuated; coronula evanescent; outer membrane of oospore with linear granulations...10. *T. glomerata*

Coronula composed of one row of five cells; antheridia produced below oogonia in monoecious species...CHARA

Ecorticate; stem and branchlets naked..................................11. *Chara Braunii*

Corticated; stem and portions of branchlets covered by a sheath consisting of longitudinal rows of cells.

Stem falsely haplostichous; secondary cells developed but extend only a short distance from the node.

Oospore ca. 580μ long, broadly elliptical, with 10-12 ridges...12. *C. evoluta*

Oospore ca. 650μ long, narrow, with 15 or 16 ridges...13. *C. hirsuta*

Stem diplostichous; secondary cells may sometimes overlap a short distance.

Primary cells prominent ....14. *C. contraria*

Secondary cells prominent..15. *C. vulgaris*

Stem falsely diplostichous; two secondary cells may be produced between primaries but one may be very short; spines single...............16. *C. excelsa*

Stem cortex very irregular but mostly diplostichous; may be haplo-, diplo-, triplostichous; spines single and in pairs................*17. C. Kieneri*

Stem triplostichous; occasionally irregular.

Lowest branchlet internode diplostichous.

Monoecious.

Cells of stem cortex equal in diameter; cortication usually regular...18. *C. globularis*

Cells of stem cortex unequal in diameter; primary cells larger and more prominent; cortication usually regular, but sometimes irregular...19. *C. delicatula*

Dioecious; cells of stem cortex about equal in diameter; stem irregularly triplostichous due to long overlapping secondary cells...20. *C. aspera*

Lowest branchlet internode ecorticate; next internode triplostichous; rarely all naked.

Antheridia and oogonia conjoined (borne at same node)............ ....21. *C. zeylanica*

Antheridia and oogonia disjoined (borne at different nodes)........ ....22. *C. sejuncta*

1. NITELLA CLAVATA (Bertero) A. Br. Char. Aust. Hook. Journ. 1:195. 1849.

For description, illustrations and citation of specimens see Daily (1). No further collections of this species are at hand from Nebraska since that report.

2. NITELLA ACUMINATA VAR. SUBGLOMERATA A. Br. Abh. Kőn. Akad. Wiss. Berl. (1882) : 36. 1883.

The treatment of this entity as a variety rather than a species is used for consistency.

Descriptions and illustrations are given in Woods (5) and Daily (1) as *Nitella subglomerata*.

Specimens seen: BOYD COUNTY: Rainwater basin, 3 mi. southeast of Naper, *27759A, 27759B* with *Chara Braunii*, Sept. 8, 1951. CLAY COUNTY: Rainwater basin, northwest of Ong, *22539*, Aug. 9, 1947. FILLMORE COUNTY: With

Chara Braunii, intermittently wet ground, 3 mi. west of Fairmont, *17161, 17162, 17163*, Aug. 15, 1944, rainwater basin, northwest of Shickley, *22550*, Aug. 9, 1947. HAMILTON COUNTY: Intermittent pool, 6 mi. west of Aurora, *17216A, 17217*, Aug. 18, 1944, *17578*, Sept. 4, 1944, *22402*, July 23, 1947.

3. NITELLA FLEXILIS (L. pro parte) Ag. Syst. Alg., p. 124, Lund, 1824.

Descriptions and illustrations are given in Woods (5) and Daily (3) under *N. flexilis* var. *flexilis*. This species was excluded from the 1944 study of the Nebraska Characeae by the author because the specimen cited by Woods upon which the report was based could not be found.

Specimen seen: BUFFALO COUNTY: Loup River pond, South of Ravenna, *20196*, May 3, 1946.

4. NITELLA OPACA Ag. Syst. Alg., p. 124. Lund, 1824.

Descriptions and illustrations are given in Woods (5) and Daily (1).

Specimens seen: DOUGLAS COUNTY: Carter Lake, Omaha, *20010, 20014*, Apr. 26, 1946.

5. NITELLA AXILLARIS A. Br. Monatsber. Kön. Akad. Wiss. Berl. (1858): 356. 1859.

Descriptions and illustrations are given in Woods (5) under *Nitella translucens* and Daily (1) under *Nitella axillaris*.

Specimens seen: CLAY COUNTY: Roadside ditch, northwest of Ong, *22540*, Aug. 9, 1947. FILLMORE COUNTY: With *Chara Braunii*, intermittent pool, 3 mi. west of Fairmont, *17162, 17163*, Aug. 15, 1944; rainwater basin, northwest of Shickley, *22346* with *C. Braunii*, July 1, 1947, *22549*, Aug. 9, 1947. HAMILTON COUNTY: Intermittent pool, 6 mi. west of Aurora, *17216*, Aug. 18, 1944, *17217* with *N. acuminata* var. *subglomerata*, Aug. 18, 1944, *22402* with *N. acuminata* var. *subglomerata*, July 23, 1947.

6. NITELLA CONFERVACEA A. Br. ex Leonh. Lotos 13:146. 1863.

For descriptions, illustrations and citation of specimens see Daily (1) under *Nitella batrachosperma* A. Br. No further collections of this species are at hand from Nebraska.

7. NITELLA OLIGOSPIRA A. Br. Monatsber. Kön. Akad. Wiss. Berl. (1858): 357. 1859.

PLATE I-A

Plants usually described as 20-25 cm. in height, but Nebraska material lacks complete plants; stem ca. 625 μ with usually 5 or 6 branchlets at a node; monoecious; fruiting bodies not enveloped in mucus; branchlets of sterile and and fertile whorls similar, usually 2-3 (4) times furcate, primary rays ca. ½—1/3 length of entire branchlet, secondary rays usually 5 or 6 at a node, tertiary rays usually 3 at a node, quaternary rays (if present) 2 or 3 at a node; ultimate rays unequal in size with some very small, 2-celled, end cell a mucro;

oogonia usually located singly at the second and third branchlet nodes; coronula persistent; oospore light brown, ca. 6 inconspicuous ridges, ca. 290 μ in length, ca. 240 μ in width; outer oospore membrane with interrupted reticulation; antheridia up to 370 μ in diameter.

Specimen seen: FILLMORE COUNTY: Rainwater basin, northwest of Shickley, *22548*, Aug. 9, 1947.

8. TOLYPELLA INTRICATA (Trentepohl ex Roth) Leonh. Lotos 13:57. 1863.

For descriptions and illustrations see Daily (2). No further collections are at hand from Nebraska.

9. TOLYPELLA PROLIFERA (Wallr.) Leonh. in Lotos 13:57. 1863.

A description and illustrations are given in Daily (2).

Specimens seen: DOUGLAS COUNTY: With *Nitella opaca*, water 8 ft. deep, Carter Lake, Omaha, *20014*, Apr. 26, 1946. LINCOLN COUNTY: Floodplain ditch, Pawnee Springs, *22311*, June 24, 1947.

10. TOLYPELLA GLOMERATA (Desv. in Loiseleur-Deslongchamps) Leonh. in Lotos 13:129. 1863.

A description and illustrations are given in Daily (2).

Specimens seen: DOUGLAS COUNTY: With *Nitella opaca*, water 8 ft. deep, Carter Lake, Omaha, *20014*, Apr. 26, 1946. SCOTTS BLUFF COUNTY: With *Chara contraria*, gravel pit pond, Scottsbluff, *22027*, *22029*, *22030*, *22037*, May 18, 1947, *23493*, May 9, 1948.

11. CHARA BRAUNII Gmel. Fl. Bad. Alsat. 4:646. Carlsruhe. 1826.

Descriptions and illustrations are given in Woods (5) and Daily (1) as *Chara coronata*.

Specimens seen: BOYD COUNTY: Rainwater Basin, 3 mi. southeast of Naper, *27759B*, Sept. 8, 1951. CHERRY COUNTY: Valentine Lakes Refuge, marshy creek below Willow Lake, *27595A*, *27595B*, Hay Lake marsh, *27613*, Aug. 27, 1951. DOUGLAS COUNTY: Carter Lake, Omaha, *17649*, Sept. 12, 1944. FILLMORE COUNTY: Intermittent pool, 3 mi. west of Fairmont, *17161* with *Nitella acuminata* var. *subglomerata*, *17162*, *17163*, Aug. 15, 1944; rainwater basin, 3 mi. northwest of Shickley, *22346*, July 1, 1947, *22548* with *N. oligospira*, 22549 with *N. axillaris* and 22551, Aug. 9, 1947. HAMILTON COUNTY: Intermittent pool, 6 mi. west of Aurora, *17216*, *17216A* and *17217* with *N. acuminata* var. *subglomerata*, Aug. 18, 1944, *17578* with *N. acuminata* var. *subglomerata*, Sept. 4, 1944, *22402* with *N. acuminata* var. *subglomerata*, July 23, 1947. HOWARD COUNTY: Loup River pool, St. Paul, *22906*, Oct. 14, 1947. LINCOLN COUNTY: Edge of spring-fed creek, Whitehorse Creek, 7 mi. north of North Platte, *17508*, Sept. 1, 1944.

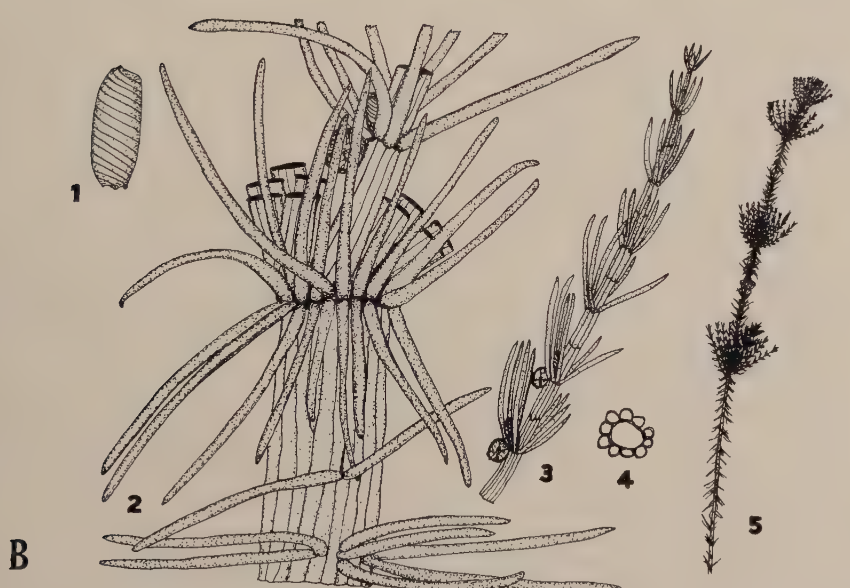

Plate I. A. NITELLA OLIGOSPIRA A. Br. 1. Small portion of outer oospore membrane. 2. End cells of ultimate rays. 3. Branchlet. 4. Oospore. 5. Coronula. 6. Portion of plant. B. CHARA HIRSUTA T. F. Allen. 1. Oospore. 2. Base of branchlet whorl. 3. Branchlet. 4. Cross section of stem. 5. Portion of plant. All drawings are enlarged except the habit sketches which are natural size.

12. CHARA EVOLUTA T. F. Allen. Bull. Torrey Bot. Club 9:41, pl. 19. 1882.

Descriptions and illustrations are given in Woods (5) and Daily (1).

Specimen seen: DUNDY COUNTY: *21209*, July 29, 1946.

13. CHARA HIRSUTA T. F. Allen. Bull. Torrey Bot. Club 27 (6):301. June, 1900.

PLATE I-B

Mature plants up to 20 cm. (some of plants not entire); sparsely branched; monoecious; ca. 10 branchlets at a stem node; stipulodes in two whorls at the base of the branchlet whorls, both upper and lower series variable in length, up to 2 mm. in length but some very short; stem cortex haplostichous (occasionally small secondary cells formed), with occasional interstices; spine cells 1-3 together, but usually 2, very variable but up to 2 mm. in length; branchlets with ca. 7 nodes, 7 singly corticated internodes (sometimes having interstices) and an ecorticate terminal cell surrounded by a tuft of bracts; bracts and bracteoles very long, 8 at the lowest branchlet node; oospore black, truncate at both ends, ca. 610—680 (720) μ long, 215—238 μ wide, with 15 or 16 ridges; antheridia up to 365 μ in diameter.

Specimens seen: SHERIDAN COUNTY: sandhill marsh pond west of Antioch, *20592*, May 23, 1946; marsh pond east of Antioch, *20615*, May 23, 1946.

Apparently this species has not been reported thus far from any location besides the type. The type specimen located at the New York Botanical Garden was seen. The Nebraska collections are very similar but have longer stipulodes, bracts, bracteoles and spine cells. In respect to these characteristics, Kiener collection *20615* is nearest the type and Kiener collection *20592* has the longest. However, in respect to plant stature, some plants of *20615* are only 8 cm. high while *20592* compares favorably with the type. After more specimens are found, it may be discovered that there is intergrading between *Chara hirsuta* and *Chara evoluta* to the extent that they should be considered one species.

It was found that the type specimen has occasionally 3 spine cells together. Also, some oospores are up to 330 μ in width. The Nebraska material, therefore, is in agreement.

14. CHARA CONTRARIA A. Br. ex Kűtz. Phyc. Germ.:258. Nordhausen, 1845.

Descriptions and illustrations are given in Woods (5) and Daily (1).

Specimens seen: BANNER COUNTY: North of Harrisburg, Pumpkin Creek, *22720*, Aug. 21, 1947; northeast of Harrisburg, pool, Bighorn gulch, *22734*, Aug. 21, 1947. BUFFALO COUNTY: In gravel pit pond, Kearney, south on Platte River, *18016*, Nov. 6, 1944; gravel pit pond, south of Kearney, *18881*, May 4, 1945; gravel pit pond, south of Gibbon, *22894*, Oct. 14, 1947; Loup

River pond, south of Ravenna, *20200,* May 3, 1946. Butler County: Sandpit pond, north of David City, *21566, 21570,* Nov. 8, 1946. Chase County: Cattle watering tank, 10 mi. west of Champion, *23582,* May 15, 1948. Cherry County: Shell Lake, northeast of Gordon, *22205,* May 26, 1947; fish hatchery pond, Valentine, *23771,* June 18, 1948; bank pools of North Loup River, near Brownlee, highway 83, *23902,* June 22, 1948. Dawes County: Chadron Creek, Chadron State Park, *20359,* May 15, 1946, *20398,* May 17, 1946; old pond, east of Crawford, *20403,* May 17, 1946; Little Bordeaux Creek, *20565,* Little Bordeaux Creek pools, *20566, 20567,* May 22, 1946; Dawson County: Sand pit lake, Lexington, *16851,* June 16, 1944. Dodge County: Gravel pit pond, Fremont State Park, *23921,* July 1, 1948. Douglas County: Floodplain pond near Carter Lake, Omaha, *17636,* Sept. 12, 1944; Carter Lake shore, Omaha, *17650,* Sept. 12, 1944, *20009,* Apr. 26, 1946, *26197, 26201,* Sept. 20, 1950. Dundy County: Ponds, Rock Creek Hatchery, *19499-19501, 19503, 19504, 19507, 19508-19510, 19512, 19516, 19517, 19519, 19526-19528, 19533, 19535, 19538,* Aug. 3, 1945; pond, Rock Creek Park, *19421, 19422,* Aug. 3 1945; Rock Creek Lake State Park, off-set pool and streamlet, *19728, 19729, 19734,* Oct. 5, 1945; Rock Creek above parks, headwater springs and marsh, *19865, 19866,* Oct. 9, 1945; *21179, 21201, 21202, 21204, 21206, 21207* with *C. aspera,* July 29, 1946. Garden County: Roadside pond, south of Oshkosh, *21105, 22014, 22015,* May 24, 1947; floodplain slough, Lewellen, 4 mi. east, *23450,* May 5, 1948. Grant County: Marsh pond, 4 mi. east of Whitman, *20661,* May 26, 1946. Hall County: Floodplain ditch, southeast of Grand Island on Platte River, *17876,* Oct. 29, 1944, *21106,* July 8, 1946, *22406,* July 23, 1947. Howard County: Loup River pool, St. Paul, *22907,* Oct. 14, 1947. Kearney County: Gravel pit pond on Platte River, north of Axtell, *18008,* Nov. 6, 1944, *18963, 18964, 18966,* May 23, 1945. Keith County: Spring seepage among mosses, Lonergan Creek, Lemoyne, *23366,* May 4, 1948; edge of seepage pond, northeast of Ogallala, *27305, 17306,* July 24, 1951; drainage ditch north of Ogallala, *27921, 27935,* Oct. 8, 1951; running water of Lonergan Creek, Lemoyne, northwest of Ogallala, *28835,* Aug. 28, 1952. Kimball County: Lodgepole Creek, Bushnell, 8 miles west, *22672,* Aug. 18, 1947; Bennet Reservoir, east of Kimball, *22699, 22700,* Aug. 18, 1947. Lincoln County: Spring-fed slough along highway, North Platte, *17298,* Aug. 24, 1944; shallow water, cut off meander, Fremont slough, 1 mile south of North Platte, *17945,* Nov. 2, 1944; mucky bottom of old shallow river pool, North Platte, on South Platte River, *17951,* Nov. 4, 1944; roadside ditch north of North Platte, *18727,* Apr. 24, 1945; island pool, North Platte River, North Platte, *18740,* Apr. 25, 1945; gravel pit pond, south of North Platte, *18775,* Apr. 27, 1945; channel pool on island, Platte River, south of Brady, *19080a, 19082,* May 29, 1945; gravel pit pond, Brady Island, *19119,* May 30, 1945. Merrick County: Sand pit pool, near Clarks, roadside park, *22917,* Oct. 15, 1947; gravel pit pond, Central City , *23913,* June 23, 1948. Morrill County:

Floodplain ditch, south of Broadwater, *22017, 22018,* May 17, 1947; floodplain ditch west of Bridgeport, *22160,* May 23, 1947; gravel pit pond, south of Bayard, *22166,* May 23, 1947; cattail marsh, southeast of Bayard, *24279,* Dec. 2, 1948; artesian spring pool, southwest of Broadwater, *24326,* Dec. 3, 1948. REDWILLOW COUNTY: Roadside ditch, west of Cambridge, *19405,* July 31, 1945. SCOTTS BLUFF COUNTY: Gravel pit pond, west of Scottsbluff, *22021, 22026, 22027, 22029, 22030, 22037-22039,* May 18, 1947; gravel pit pond, Scottsbluff, *22042, 22051, 22068,* May 20, 1947; gravel pit pond, west end of Scottsbluff, *23492, 23493* with *Tolypella glomerata,* May 9, 1948; seepage, Akers Draw, northeast of Morrill, *25112,* Nov. 22, 1949. SHERIDAN COUNTY: Marsh pond, west of Antioch, *20593,* May 23, 1946; roadside marsh pond, east of Lakeside, *20616,* May 23, 1946. SHERMAN COUNTY: Floodplain pond, Loup City, *24222,* Nov. 3, 1948. SIOUX COUNTY: Seepage ponds, Sheep Creek spring, 3 mi. north of Henry, *23521,* May 10, 1948.

15. CHARA VULGARIS Vaill. ex L. Sp. Pl., p. 1156. Stockholm, 1753.

Illustrations and descriptions are given in Woods (5) and Daily (1) under the name *Chara foetida* A. Br.

Specimens seen: BANNER COUNTY: Game preserve pond, north of Harrisburg, *22140,* May 22, 1947. BUFFALO COUNTY: Loup River pond, south of Ravenna, *20197,* May 3, 1946; pool of Sweetwater Creek, south of Ravenna, *20818* with *Chara delicatula,* May 29, 1946. CHEYENNE COUNTY: Lodgepole Creek, Potter, 5 mi. east, *22602,* Aug. 16, 1947. DUNDY COUNTY: Rock Creek hatchery, *19514,* Aug. 3, 1945; *21200, 21203,* July 29, 1946. KEITH COUNTY: Floodplain ditch, North Platte River, west end of county, *22476,* July 27, 1947; drainage ditch, north of Ogallala, *27918, 27919,* Oct. 8, 1951. SCOTTS BLUFF COUNTY: Gravel pit pond, west end of town, Scottsbluff, *22031,* May 18, 1947; gravel pit pond, Scottsbluff, *23494,* May 9, 1948; seepage, Akers Draw, northeast of Morrill, *25112* with *C. contraria,* Nov. 22, 1949.

16. CHARA EXCELSA T. F. Allen, Bull. Torrey Bot. Club 9(4):43. Apr., 1882.

A description and illustrations are given in Daily (3).

Specimens seen: GRANT COUNTY: Sandhill marsh pond, 5 mi. east of Hyannis, *20643,* May 26, 1946. SHERIDAN COUNTY: Marsh pond, west of Antioch, *20595, 20600,* May 23, 1946.

17. CHARA KIENERI Daily. Butler Univ. Bot. Stud. 9:127-130. 1949.

The type specimen was collected in Nebraska.

Specimens seen: GRANT COUNTY: Marsh pond, 4 mi. east of Whitman, *20662,* May 26, 1946. SHERIDAN COUNTY: With *Chara aspera,* marsh pond, west of Antioch, *20591A,* May 23, 1946.

18. CHARA GLOBULARIS Thuill. Flor. Env. Paris, ed. 2, p. 472. 1799.

Descriptions and illustrations are given in Woods (5) and Daily (1) under the name *Chara fragilis* Desv.

Specimens seen: Buffalo County: Gravel pit pond, Gibbon, *17880,* Oct. 29, 1944. Cheyenne County: Pool in Lodgepole Creek, east of Potter, *22627,* Aug. 16, 1947. Douglas County: Carter Lake, Omaha, *17648, 17649,* with *C. Braunii* Sept. 12, 1944; sand pit pond, Valley, *26146,* Sept. 20, 1950. Dundy County: Fish ponds, Rock Creek Hatchery, *19535,* with *C. contraria,* Aug. 3, 1945; *21208* with *Chara aspera,* July 29, 1946. Grant County: Sandhill marsh pond, Hyannis, 5 mi. east, *20643* with *C. excelsa,* May 26, 1946. Sheridan County: Sandhill marsh pond, east of Lakeside, *20617, 20618,* May 23, 1946. Webster County: Pond of Pawnee Recreation Ground, west of Guide Rock, *11055a,* Aug. 14, 1941.

19. CHARA DELICATULA Ag. Syst. Alg., p. 130. Lund, 1824. (non Desv.).

A description and illustrations are given in Daily (1) under the name *Chara verrucosa* Itzig:

Specimens seen: Buffalo County: Pool of Sweetwater Creek, south of Ravenna, *20818,* May 29, 1946. Sheridan County: Marsh pond west of Antioch, *20598, 20599,* May 23, 1946.

20. CHARA ASPERA Willd. Ges. Naturf. Fr. Berl. Mag. 3:298. 1809.

The descriptions and illustrations given in Daily (1) are of the var. *Macounii* Allen. Typical material having long spines, bracts, bracteoles and stipulodes has been found in Nebraska since then.

Specimens seen: Dundy County: Fish ponds, Rock Creek Hatchery, *19502,* also collections with *Chara contraria 19507, 19510,* and *19533*, Aug. 3, 1945; *21207, 21208,* July 29, 1946. Sheridan County: Marsh pond west of Antioch, *20591A, 20591B, 20592* with *Chara hirsuta, 20593* with *C. contraria, 20598* and *20599* with *C. delicatula,* May 23, 1946.

21. CHARA ZEYLANICA Willd. Mem. Acad. Roy. Sc. Berl. (1803):86. 1805. Berlin.

A description and illustration are given in Daily (1) under the name *Chara gymnopus*. Since confusing intermediates occur, the forms of this species are difficult to separate. However, probably two forms, *macilenta* (A. Br.) Daily, and *Michauxii* (A. Br.) H. & J. Groves, are represented in the specimens below.

Specimens seen: Dodge County: Sand pit lake, Fremont, *21476,* Aug. 29, 1946. Douglas County: Shallow water, Carter Lake, Omaha, collected by *Howard L. Wiegers, Kiener* Col. No. *21519*, Aug. 31, 1946, *26194, 26196,* Sept. 20, 1950.

22. CHARA SEJUNCTA A. Br. in G. Engelmann and A. Gray. Plantae Lindheimerianae. Bost. Jour. Nat. Hist. 5:264. 1845.

For description and illustrations see Woods (5) and Daily (1). No further collections are at hand from Nebraska.

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5. WOODS, ALBERT F. University of Nebraska. Flora of Nebraska. Published by the Botanical Seminar. Part II. Coleochaetaceae, Characeae. 1894.

NOTES ON THE ALGAE—IV

WILLIAM A. DAILY
Butler University

The specimens cited here are to be found in the writer's personal herbarium which is on file in the Herbarium of Butler University, the Cryptogamic Herbarium of the Chicago Natural History Museum and the personal herbarium of Francis Drouet, Chicago.

IV—DINOPHYCEAE

PERIDINIUM VOLZII f. VANCOUVERENSE (Wailes) Lefèvre, Lefèvre, 1932. 78, 183, Figs. 895-898. Syn. *P. striolatum* Wailes, Vancouver, Museum Notes, III, 1928, p. 7, (not *P. striolatum* Playfair); *P. vancouverense* Wailes, Ann. Protistol., III, 1931, p. 110.

According to available published reports, *Peridinium volzii* f. *vancouverense* (Wailes) Lefèvre heretofore has been found in British Columbia loc. cit., Australia [1] and Minnesota [2]. Indiana is now added to that list.

The type specimen collected in Vancouver, British Columbia, is not available for study at the University of British Columbia or the Pacific Biological Station at Nanaino. Apparently types of dinoflagellates were not kept by G. H. Wailes.

Further unsuccessful attempts were made to borrow typic or otherwise authenticated specimens relating to the Australian and Minnesota reports.

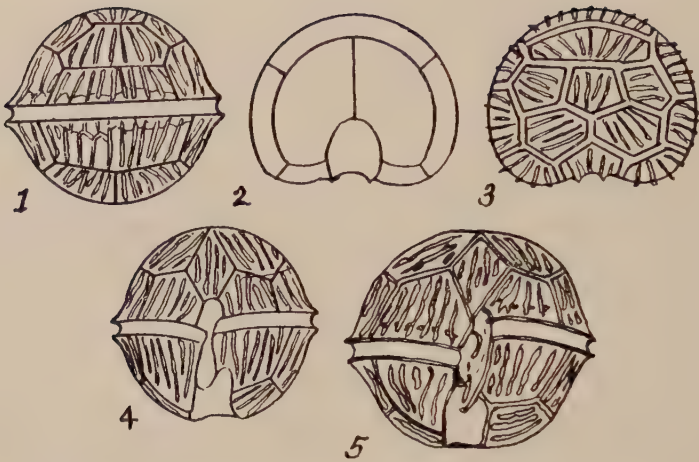
The Indiana dinoflagellate (see fig. 5) resembles very closely the description and drawings (see figs. 1-4) of *Peridinium striolatum* loc. cit., however, the maximum length and width of the former are 72 μ instead of 65 μ as noted for Wailes' specimen.

Specimens seen: INDIANA: ELKHART COUNTY: With *Ceratium Hirundinella* (O.F.M.) Schr., *Fragilaria crotonensis* Kitton, *Gomphosphaeria aponina* Kütz and *Botryococcus Braunii* Kütz. Net collection from Round Lake, 2 miles north of Bristol, *F. K.* & *W. A. Daily* 2626, Aug. 27, 1952, net collection, *F. K.* & *W. A. Daily 2745*, July 14, 1955.

I wish to thank J. V. Prohaska, M.D., owner of Round Lake, for collecting

[1] Playfair, G. I. Peridineae of New South Wales. Proc. Linn. Soc. New South Wales. 44:793-818. 1919 (1920).

[2] Eddy, S. The Freshwater Armored or Thecate Dinoflagellates. Trans. Amer. Microsc. Soc. 44:277-321. 1930.



Figs. 1-4. *Peridinium striolatum* Wailes. Holotype. Dorsal, antapical, apical and ventral views. (From Wailes).

Fig. 5. *Peridinium volzii* var. *vancouverense* (Wailes) Lefèvre. F. K. and W. A. Daily collection no. 2745. Ventral view.

privileges; Dr. Rufus Thompson for verifying the identification of the alga and Dr. Robert F. Scagel, Institute of Oceanography, University of British Columbia, Vancouver, for providing pertinent information and printed matter. The drawings of *P. striolatum* Wailes were reproduced with the permission of T. H. Ainsworth, Curator of the City Museum, Vancouver, British Columbia. Suggestions and aid of Mrs. Fay K. Daily and Dr. Francis Drouet are gratefully acknowledged.

THE EFFECTS OF VARIOUS PHYSICAL AND CHEMICAL AGENTS ON A STAPHYLOCOCCUS BACTERIOPHAGE

DONALD H. HOLMES

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In recent years considerable attention has been focused on a group of organisms known as bacterial viruses or bacteriophages. These minute virus particles are parasitic upon bacterial cells and probably most bacteria are susceptible to one or more of them. There are several excellent reviews and symposia covering the various steps of bacteriophage multiplication and the effects of inhibiting agents (1, 29, 30). The reader is referred to them for an explanation of the processes involved in attachment to and multiplication within the host cell.

The experimental work in this paper is divided into two sections: (1) the effect of physical agents and (2) the effect of chemical agents on a staphylococcus bacteriophage. The physical treatments include thermal inactivation, ultrasonic vibration, lyophilization, long term storage, effect of temperature on adsorption rate and photoreactivation after exposure to ultraviolet light. Chemical treatments included suspension in various salt solutions and the effect of several pH values on phage stability. It is apparent that some of these procedures could be classified as either physical or chemical in action or more properly as physico-chemical. However, for the purpose of this paper the more simple distinction will be followed beginning with the effects of physical agents. Preliminary experiments had shown that the phage used was inactivated in 30 minutes when suspended in broth at 60° and that it gradually loses activity when stored in broth at 4°. High speed centrifugation procedures also cause rapid inactivation.

GENERAL MATERIALS AND METHODS

Media: Tryptose phosphate broth (TPB) was used to grow the host organism and as a diluent. One percent base layer agar plates, 1.5% agar slants and 0.7% top layer agar tubes were prepared by adding sufficient agar to the TPB. All media were sterilized by autoclaving 15 minutes at 15 pounds. The final pH was 7.4.

Phage and Host Bacterium: The host bacterium SK9 and the phage P1 are isolates from cultures used routinely in antiphage assays at Eli Lilly and Company. Lysates of SK9 by P1 titer from 5 to 7 x 10^9/ml. after Selas filtration.

Phage Titering: The P1 samples were titered using the method described by Adams (1). The plates were inverted, then incubated overnight at 37° and counted on a Quebec colony counter.

ADSORPTION RATE AT VARIOUS TEMPERATURES

The first step in virus multiplication is adsorption, or attachment to the surface of the host cell prior to penetration of the cell membrane. Information regarding the adsorption phenomenon is of value since this action or a similar series of events is assumed to be universal among all plant, mammalian or bacterial viruses as the initial step in infection of the host cell.

Material and Methods: SK9 was grown in TPB to 2 x 10^7 organisms/ml., centrifuged and resuspended in an equal amount of physiological saline. The phage was diluted to 1 x 10^8/ml. in saline and both phage and host organism were brought to the desired temperature before mixing. At t=O, one ml. of P1 was added to nine ml. of SK9 and the tube was shaken. One half ml. samples were removed at intervals then diluted 1/2000 in saline at 2° to stop further adsorption. A phage titer was taken to determine the original titer and the samples were centrifuged 10 minutes at 5900g. The supernate was titered. Velocity constants were computed from the formula:

$$k = \frac{2.3}{t \text{ x cell count}} \text{ x log } \frac{\text{initial phage titer}}{\text{final phage titer}}$$

Results and Discussion: Velocity constants for the attachment of P1 to SK9 in saline range from 489 x 10^{-12} cm^{3} min^{-1} at 1° to 729 x 10^{-11} at 45° (fig. 1). At a given temperature the maximum rate of virus adsorption is attained and additional increases in temperature do not result in a correspondingly larger velocity constant. The maximum rate of adsorption for this system lies between 28° and 37° since no increase occurs above the higher temperature. This same effect was shown by Puck, et al. (2) with coliphage T1 in broth or buffer with Mg++ where adsorption reaches a maximum around 37° and falls off with decreasing or increasing temperatures. In addition to the temperature effect adsorption is influenced by the presence of certain co-factors and salts and the physiological condition of the host cell.

LONG TERM STORAGE

Information regarding the ability of microorganisms to remain viable when stored under various conditions is of prime importance. Long term storage of cultures can be best accomplished by first freeze-drying the material. The results found using this technique with P1 are described elsewhere in this paper. However, bacteriophage suspended in liquid remains viable for some time. It is with this type of storage that the following experiments were concerned.

Material and Methods: A freshly prepared phage stock was diluted to approximately 4 x 10^5/ml. in broth (pH 7.4), saline (pH 6.8) and in distilled water (pH 6.8). A sample of each was stored at 4°, room temperature (23°) and 37° in stoppered test tubes. Titers were made at intervals.

Results and Discussion: P1 was completely inactivated in three days when suspended in distilled water at room temperature or 37°. Rapid inactivation also occurs at 4° in water as only 10% was active after one week. In four weeks over 99.9% was inactive. P1 was found unstable at 37° or room temperature in saline and is 60% inactivated after one week at 4°. The least inactivation occurs when P1 is held in TPB. In this medium 90% of the phage is lost in one week at 37°. Only 1% remains active after two months at room temperature. When P1 is suspended in TPB and stored at 4° it loses very little titer in three weeks. In two months the titer drops to 20% of the original value. This phage can be stored in broth for short periods but a considerable titer drop is to be expected. Freeze-drying of stock preparations is preferable in order to retain viable phage particles.

LYOPHILIZATION

Several bacteriophages have been lyophilized with varying success. Six dysentery phages were prepared using this procedure by Schade and Caroline (3, 4, 5). Five of these six lost no activity after one year over a dessicant at 37°. Coliphage T6, grown in synthetic media and lyophilized by Putnam, et al. (6) was inactivated. Many mammalian viruses resist freeze-drying and were found viable after years of storage. Hofstadt, et al. (7) and Scherp, et al. (8). Bacteriophage P1 was lyophilized using standard procedures.

Material and Methods: Freshly prepared lysates were filtered through an 02 Selas candle and titered. Twenty-five ml. were placed in a round bottom flask and rapidly shell frozen in an alcohol/CO_2 bath. The freezing required less than one minute. The flask was atached to a lyophilization apparatus, evacuated and dried for 21 hours. At the conclusion of the drying process the material, in the form of brown flakes, was scraped off the sides of the flask, weighed, and placed in a tightly stoppered tube. Other phage lysates were first dialized at 4° in saline or water then lyophilized.

Results and Discussion: Approximately 85% of the phage is lost in the process of lyophilization. An additional 6% loss occurred in storage after 30 days but no further decrease was seen during six additional months at 4°. In spite of such a large drop in phage activity no difficulty was experienced in preparing fresh P1 lysates from the lyophilized material. Lysates which had been dialyzed in water or saline before freeze-drying lost no titer. When these preparations were lyophilized and then reconstituted in either saline or TPB over 99% of

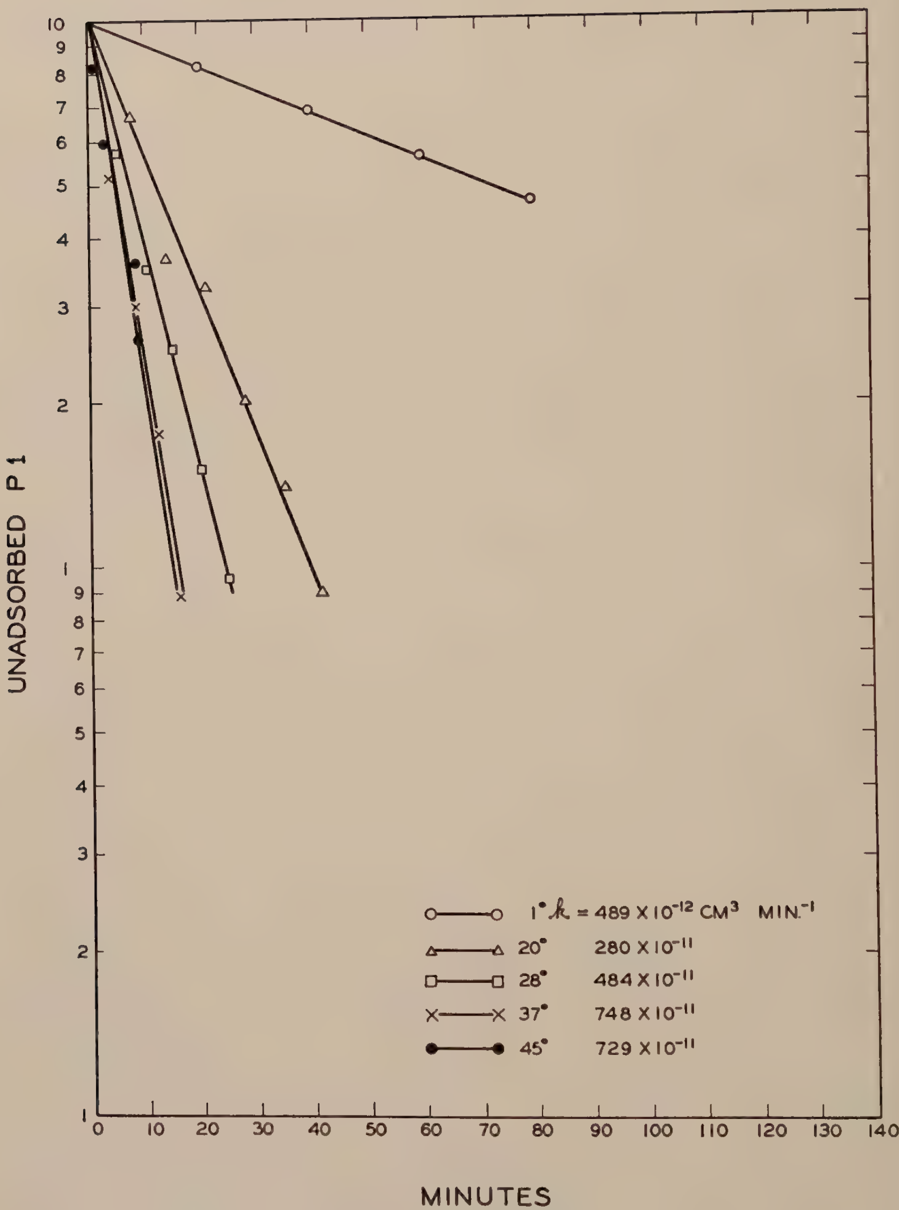


FIGURE 1

The effect of heat on the adsorption rate of PI bacteriophage to its host cell *S. aureus* SK9 in saline.

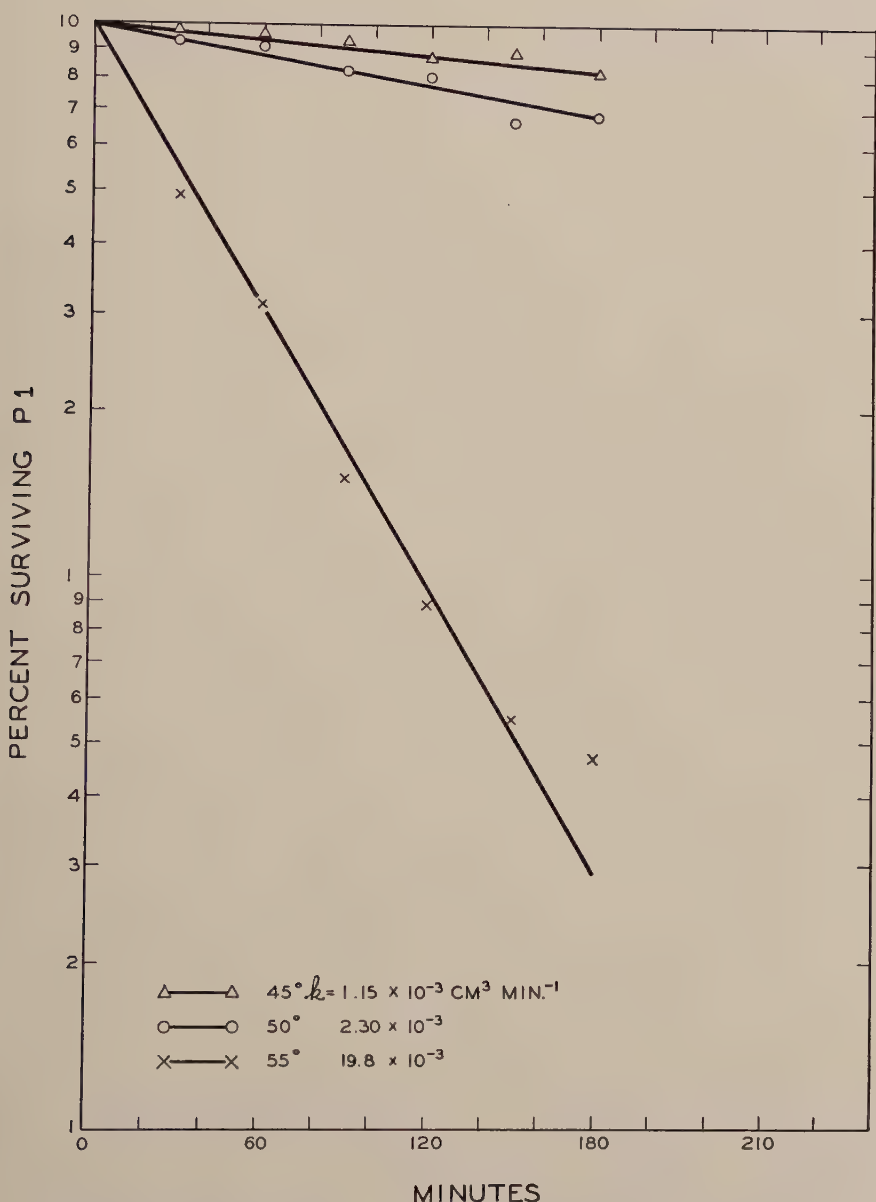
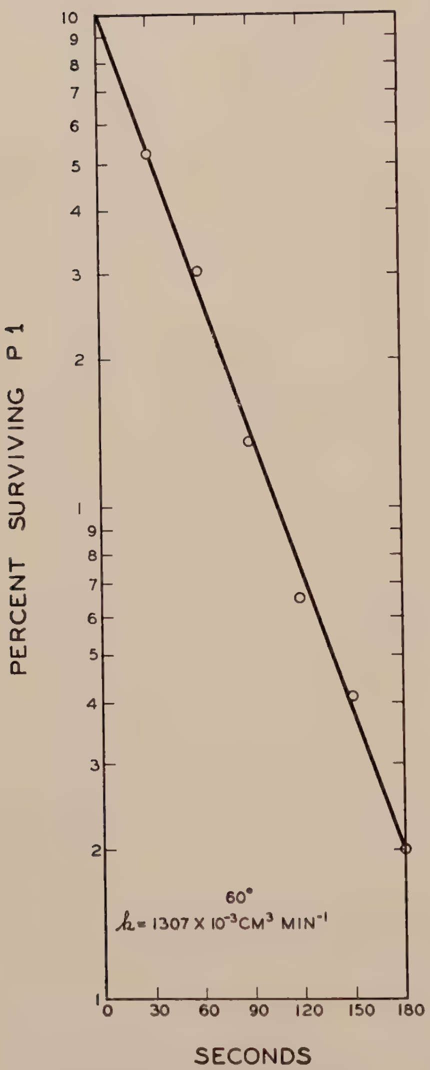


FIGURE 2

Log of uninactivated bacteriophage PI in broth at various temperatures as a function of time. 45°-55°.



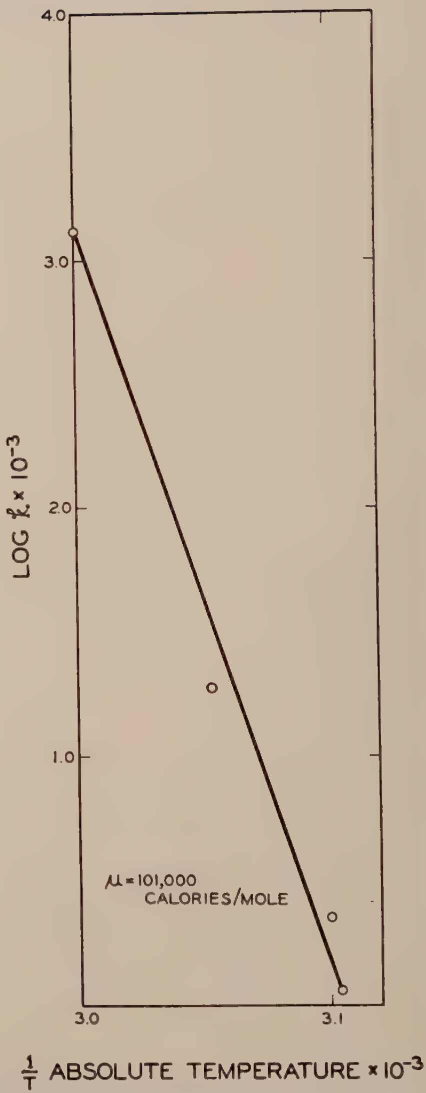


FIGURE 3
Log of uninactivated bacteriophage PI in broth at 50° as a function of time.

FIGURE 4
Log of the first order specific reaction rates for inactivation of PI bacteriophage as a function of temperature.

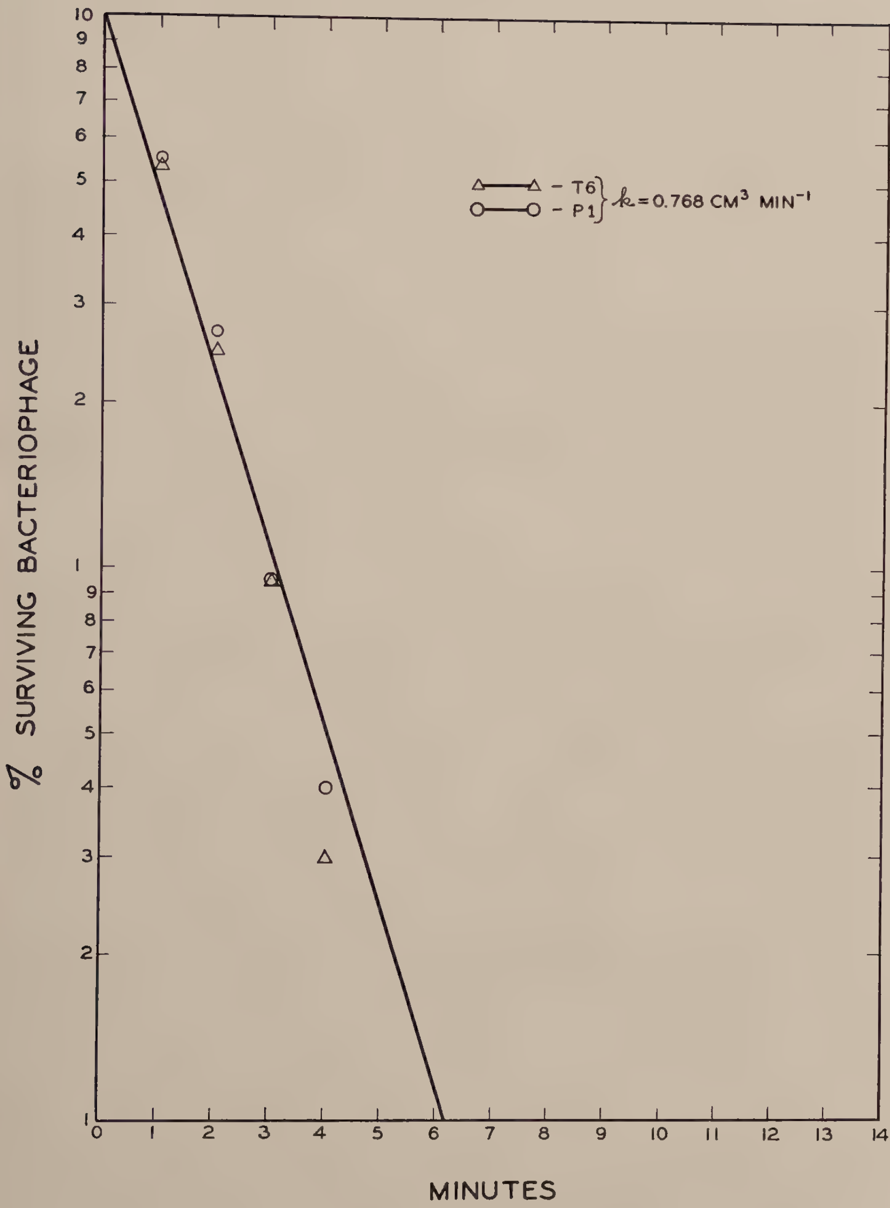


FIGURE 5

Log of uninactivated bacteriophages PI and T6 in broth treated with radio frequency oscillation as a function of time.

the phage was found to be inactivated. If P1 were lyophilized in ampoules under vacuum or dry nitrogen assuring the complete absence of moisture no doubt its stability would be greatly increased.

ULTRA-SONIC VIBRATION

Bacteriophages and other viruses have been shown to be very vulnerable to the effects of high frequency vibration. Such inactivation usually proceeds as a first order reaction.

Materials and Methods: The phage was diluted in TPB and 50 ml. placed in the water cooled Raytheon Magnetostriction sonic oscillator (Model DF-101). The frequency produced by this instrument is 10,000kcs. One tenth ml. samples were removed at intervals, diluted and plated. A sample of T6 coliphage was also prepared and treated in the same manner in order to compare the sonic effects on both phages. Velocity constants were determined using the formula,

$$k = \frac{2.3}{t} \times \log \frac{\text{initial phage titer}}{\text{final phage titer}}$$

cited in Pollard and Reaume (12).

Results and Discussion: P1 was found to be inactivated at approximately the same rate as the coliphages T2, T4, T5 and T6 and megatherium phages M2 and M3. In one minute one half of the phage was destroyed and only 2% remained active after five minutes exposure (fig. 5). All of the T series of coliphages have been subjected to this form of inactivation by Anderson, et al. (9). He found T2, T4, T5 and T6 to be more rapidly inactivated than the smaller phages T1, T3 and T7, and suggested that the larger, more complex phages were more susceptible to sonic action. Friedman and Cowles (10), working with a group of five *B. megatherium* phages could find no relationship between size and relative sensitivity to sonoration. A staphylococcus phage was reported by Krueger (11) to be over 99% inactivated after 10 minutes exposure to high frequency vibration. Velocity constants for both P1 and T6 were $0.77 cm^3 min^{-1}$.

THERMAL INACTIVATION

Velocity constants for the heat inactivation of various phages have been determined. Cherry (13) investigated the effect of heat on a *Streptococcus lactis* phage at temperatures from 30 to 65°. Other workers, Chang, et al., (14), Pollard and Reaume (15) and Adams (16) observed the effects of heat on the coliphage series. Friedman and Cowles (17) ran heat inactivation curves on their group of *B. megatherium* phages. In this paper a series of experiments were performed with P1 at temperatures of from 45 to 60°.

Materials and Methods: P1 was diluted in broth to 5 x 10^6/ml. One tenth ml. was added to a tube containing 9.9 ml. of TPB which had been previously brought to the desired temperature in a thermostatically controlled water bath. The tube was shaken, samples removed at intervals, diluted immediately in chilled TPB, then plated. The rate of inactivation (k) was calculated from the inactivation curves (figs. 2 and 3) for each temperature using the velocity constant equation. The logarithms of the k values for each temperatures were plotted against the reciprocals of the corresponding absolute temperatures in the manner developed by Arrhenius in order to illustrate the relationship between reaction rate and temperature.

Results and Discussion: Seventeen percent of the phage P1 was inactivated at 45° for 180 minutes and approximately twice that amount was dead at 50° for the same length of time. When P1 was treated at 55° for 180 minutes 97% of the phage was destroyed (fig. 2 and 3). Experiments performed at 65° indicate that over 99% was lost in less than 30 seconds. Velocity constants were not prepared for this temperature due to the difficulty in performing accurate sampling. Velocity constants (k) range from 1.15 x $10^{-3}cm^3min^{-1}$ at 45° to 1307 x 10^{-3} at 60°. All thermal inactivation studies for this phage compare well with those found by Krueger (17) in 1932 for a staphylococcus phage. The temperature characteristic of thermal inactivation (μ) has not been determined for all phages subjected to heat inactivation. In some cases the curve was not linear over its entire length. Cherry (13) found his S. *lactis* phage to have a μ value of 11,000 calories between 30 and 55° with an increase to 76,000 calories from 55 to 65°. The coliphage studies by Chang et al. (14) also had a non-linear curve with two μ values. The value of μ found for P1 was 100,000 calories and the curve was linear. This figure was also found by Krueger (17) with a staphylococcus phage (fig. 4).

PHOTOREACTIVATION

A description of the phenomonon known as photoreactivation (PHTR) of bacteriophages was first published in 1949 by Dulbecco (18). He found that all of the T coliphages, after exposure to ultraviolet light and plating on susceptible host cells, would, if incubated under strong visible light, result in higher titers than similarly treated coliphages incubated in the dark. Pre-illumination of the host cells or of the irradiated phage with visible light resulted in no PHTR and irradiated phage could only be reactivated after adsorption to the host cell. Hill and Rossi (19) working with a dried preparation of phage T1, showed that no PHTR took place with the dry material. They concluded that PHTR was dependent upon the state of the phage at the time of exposure to ultraviolet light. Dulbecco (18) and Watson (20) found no PHTR to occur in phage which had been treated with x-rays. PHTR in P1 staphylococcus phage was shown to occur in the following experiments.

Materials and Methods: P1 was irradiated using a 15 watt GE germicidal lamp with a filter giving maximum emission at 2570 A. Samples of phage diluted in TPB were exposed for periods of from three to three and one half minutes so as to cause approximately 80% inactivation. The irradiated phage was titered on 12 plates. Four were immediately placed in total darkness, four were placed beneath one 40 watt fluorescent lamp at a distance of 26 cm. and four beneath two 40 watt lamps at the same distance. All plates were incubated at 26° for 18 hours and then counted.

Results and Discussion: In these experiments reactivation titers amounted to twice the titer of the irradiated phage not treated with visible light. Titers of irradiated phage not reactivated averaged 15% of the original untreated phage but exposure to two fluorescent lamps for 18 hours resulted in titers equal to 29% of the untreated original phage. This effect has not previously been demonstrated using a staphylococcus phage. It is interesting to note that exposure of the irradiated phage to the visible light produced by one lamp did not cause the reactivation that two lamps produced in the same length of time. Also, if phage plates previously exposed to one lamp received additional visible light after the initial 18 hour period no additional reactivation occurred (table III). The maximum PHTR occurs in 18 hours or less but the total PHTR for a given period is dependent upon the intensity of the illumination for that period. Perhaps, and this possibility was not investigated, the only time when PHTR actually takes place is during the adsorption of the irradiated phage particle immediately after plating and all subsequent visible light treatment has no effect on phage titer.

HYDROGEN ION CONCENTRATION

Friedman and Cowles (10) found two of five *B. megatherium* phages to be stable for one hour at 37° in broth at pH 6 to 9 and one each stable from pH 5 to 9, 5 to 10 and 6 to 10. Purified coliphage T1 is most stable at pH 6 but little loss of titer occurs at pH values of from 4.3 to 7 after 24 hours in broth (Pollard and Reaume, 15). T7 is most stable from pH 6 to 8 (Kerby, et al. 21) and T6 is stable from pH 4.9 to 8.6 (Putnam, 22). No information regarding the stability of staphylococcus phages over a range of pH was found in the literature.

Materials and Methods: Bacto tryptose and NaC1 were dissolved in water, brought to the desired pH, and sterilized in the autoclave. Glucose and Na_2HPO_4 were dissolved separately in water and sterilized, cooled and added to the tryptose-NaC1 solution. Hydrochloric acid (0.1M) and NaOH (0.1M) were employed where necessary in adjusting to the exact pH. The phage was diluted in the appropriate pH broth, then held in a 37° water bath or stored at 4° for 24 hours. Samples were removed at one and 24 hours for titering.

TABLE I

The effect of various pH values on PI bacteriophage suspended in broth.

		pH Value									
	Percent P1 active after:	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Samples held	1 hour	0	0	86	95	98	51	35	0	0	0
at 37°	24 hours	0	0	16	60	72	44	5	0	0	0
Samples held	1 hour	0	96	100	100	95	67	63	0	0	0
at 4°	24 hours	0	79	96	96	98	49	51	0	0	0

TABLE II

The effect of various concentrations of NaCI on PI bacteriophage at 37°.

Percent P1 active after	**Molar Concentration of NaC1**								
	4	**3**	**2**	**1**	10^{-1}	10^{-2}	10^{-3}	10^{-4}	10^{-5}
1 hr.	94	95	94	88	88	82	76	74	36
24 hrs.	22	24	27	24	28	24	6	4	5

TABLE III

Photoreactivation of irradiated bacteriophage PI.

	Exp. 1	Percent of Untreated Titer	Exp. 2	Percent of Untreated Titer	Exp. 3	Percent of Untreated Titer
Phage titer before irradiation	2.76×10^4		4.20×10^4		5.89×10^3	
Irradiated 3½ minutes, plates incubated in darkness	4.15×10^3	15	5.34×10^3	13	9.20×10^2	16
Irradiated, plates incubated under one 40 watt lamp	4.88×10^3	18	9.03×10^3	22	1.30×10^3	22
Irradiated, plates incubated under two 40 watt lamps	7.02×10^3	26	1.24×10^4	30	1.85×10^3	30

Results and Discussion: P1 was found to be relatively stable from pH 5 to 7 for one hour at 37° dropping off sharply at pH 4 and down to 35% at pH 9. All the phage was inactivated at pH values below 5 and above 9. A 25% drop in titer was seen when P1 was held in pH 7 TPB for 24 hours at 37°.

P1 in TPB at 4° was inactivated at an expected slower rate. Little titer loss occurred at pH's from 4 to 7 after one hour but complete inactivation occurred at pH 3 and pH 10. The phage remained stable after 24 hours at 4° in pH 5 to 7 in TPB. Fifty percent was destroyed at pH 8 (table I). In general, both mammalian viruses and bacteriophages are most stable when held in suspensions at pH values near neutrality. The zone of pH stability, however, varies over a range of pH 4 to 10 with very few viruses surviving except for short periods at pH's above 10 or below 4.

CITRATE ION

Several phage systems have been examined regarding the effect of citrate ions on adsorption and multiplication. It was suggested at one time that the classification of these organisms could be partially based on their behavior in the presence of citrate (Burnet, 23). Multiplication of coliphages T1 and T5 is inhibited in the presence of citrate but adsorption is uneffected (Adams, 24). None of the other T series phages are effected. Burnet and McKie (25) studied a large group of dysentery-Salmonella phages and found considerable variation in regard to citrate sensitivity. Rountree (26) divided a number of staphylococcal phages into sensitive and insensitive groups. All five of the megatherium phages examined by Friedman and Cowles (10) were sensitive to varying degrees.

Material and Methods: Top layer agar tubes and bottom layer agar plates were prepared containing from 10^{-1} to 10^{-4}M sodium citrate. P1 was diluted in TPB to 5 x 10^{3}/ml. then titered using the citrate agar. Controls were titered on standard TP agar.

Results and Discussion: The multiplication of P1 on the host cell was not inhibited by any concentration of sodium citrate tested.

DIVALENT SALTS

Burnet and McKie (25) investigated the effect of heat and salt concentration on a group of *Salmonella* and dysentery phages and found dilution in sodium, potassium or ammonium salts resulted in rapid loss when the phage was heated at 60°. The addition of small quantities of divalent salts such as calcium, magnesium or barium partially or completely prevented this inactiva-

tion. The addition of any one of four divalent salts at 10^{-3} M prevents phage loss at 37° for one hour on three megatherium phages (Friedman, 27). The other two megatherium phages were only partially stabilized by the same salts. All except Hg++ and Pb++ had a definite protective effect on coliphage T5 in saline (Adams, 24).

Material and Methods: All divalent salts were prepared in 0.15 M NaCl and brought to pH 7. The phage was diluted and added to the salt concentrations then incubated at 37° in a water bath. Titers were made at one and 24 hours.

Results and Discussion: P1 was completely inactivated in one hour at 37° in the presence of 10^{-2} or 10^{-3} M Cu++, Pb++, or Fe++ ions and lost 80% in 10^{-2} M Cd++. None of the other salts used at these concentrations prevented inactivation any more than the 0.15 M NaCl control. The stability of P1 is not increased when diluted in divalent salt solutions.

SODIUM CHLORIDE

Only one group of phages has been examined for the effect of different NaCl concentrations on phage stability. This group consisted of the five *B. megatherium* phages studied by Friedman (18). Four of these phages were inactivated completely in NaCl concentrations of from 10^{-1} to 5×10^{-2} M after one hour at 37°. All were stable for the same length of time in 1 M solutions.

Material and Methods: Salt solutions were prepared using reagent grade NaCl dissolved in deionized water. The phage was diluted in deionized water to the desired concentration then 0.1 ml. was added to the tubes containing 9.9 ml. of each salt solution at 37°. Incubation was continued at 37° and titers were made at one and 24 hours.

Results and Discussion: In one hour at 37° from 5% to 26% of the P1 had been inactivated in the solutions containing from 4 M to 10^{-4} M NaCl. The least inactivation occurred at NaCl concentrations of 2 M to 4 M. Approximately 75% of the phage was lost in 24 hours at salt concentrations of 4 M to 10^{-2} M and over 90% at 10^{-3} M to 10^{-5} M (table II).

SUMMARY

A staphylococcus bacteriophage lysate was treated with various physical and chemical agents and the following results were obtained:

Bacteriophage P1 is inactivated by heat at a logarithmic rate and possesses a temperature characteristic (μ) of 100,000 calories/mole. Inactivation by

high frequency oscillation is a first order reaction with a velocity constant of 0.77 cm^3min^{-1}. Photo-reactivation occurs when ultraviolet treated P1 is exposed to strong light in the visible spectrum. Adsorption constants of P1 to SK9 range from 489×10^{-12} at 1° to $748 \times 10^{-11} cm^3min^{-1}$ at 37°. P1 is most stable at pH values from 5 to 7. Of the mono- or divalent ions tested, none contributed significantly to the stability of the phage; the presence of citrate ions does not prevent phage multiplication. If P1 is held at 4° in TPB little loss of titer occurs in one month. P1 can be successfully lyophilized but there is considerable loss in the process.

ACKNOWLEDGMENTS

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EXPRESSION OF THE GENE d_1 IN THE FIRST THREE LEAVES OF *ZEA MAYS* L.

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The present study is a continuation of investigations of expression of the gene dwarf-one (d_1) in the early stages of ontogeny in maize. An earlier study indicated no visible influence of the gene at the mature embryo stage (Pelton 1954), although expression appears as early after germination as the first stages of development of the mesocotyl (Hansen 1950, Hansen and Abbe 1943). The objective of the present study is to explore the expression of d_1 in those stages of seedling development which include maturation of the first three leaves.

History of the gene d_1 dates back to 1910 when the first mutant individuals were discovered in the Cornell breeding plots (Emerson 1912). These dwarfs were later described to be the result of a simple Mendelian recessive, located on the third chromosome (Emerson, Beadle, and Fraser 1935). An early quantitative study determined that the homozygous recessive dwarfs at maturity are shorter in stature and have shorter and wider leaves than do their normal sibs (Abbe, L. B. 1936). Since then there have been several studies on the morphogenetic effects of the gene (Abbe and Phinney 1940, 1942, Hansen and Abbe 1943, Phinney 1946, Hansen 1950, Olmsted 1951, Pelton 1954, Stein 1955). The present investigation concentrates on the expression of the gene in the seedling stage of ontogeny.

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MATERIALS AND METHODS

Source of Materials

The maize kernels used in the present study were produced by a morphogenetic project directed by Dr. E. C. Abbe of the University of Minnesota Department of Botany. Five generations of backcrossing of d_1 to University of Minnesota station inbred A188 assured a fairly homogeneous background for the mutant gene. The resulting segregating offspring were selfed in 1951. Two lots from sister plants of this 1951 planting were the basis of the present

experiments. A more detailed explanation of the breeding program is given in a previous paper (Pelton 1954).

Experimental Methods

Experiments were conducted in the Oberlin College greenhouse. Three plantings were made in April and May of 1953, yielding 91 normal and 31 dwarf plants upon which the present study was based. Before planting in standard flats filled with loam soil the kernels were soaked in distilled water for twenty-four hours at room temperature. Identification by phenotype of the homozygus recessive plants is certain by the tenth day after germination. Soon after the leaves appeared daily measurements of maximum length and width of the first three leaves of normal (D_1D_1, D_1d_1) and dwarf (d_1d_1) individuals were recorded. Measurements used in analysis were those at maturity of length and width of the three leaves. The dates of maturity of these dimensions were also included in the analysis. Maturity of the leaves was assumed to have been reached when dimensions remain unchanged for three successive days.

RESULTS

Leaf Length. Mean lengths of the first three seedling leaves (referred to as leaves 1, 2, and 3 respectively) of dwarf and normal plants are presented in Table I and illustrated in Figure 1.

A marked shortness of the dwarf leaf when compared with the comparable leaf of its normal sib is apparent. The pattern of this difference is one of increasing relative expression of d_1 in successive leaves (Figure 1). The mean length in leaf 1 in the normals is 11.6 mm greater than that of the dwarfs, while leaves 2 and 3 of the normals average respectively 36.0 mm and 87.0 mm longer than the corresponding leaves to the dwarfs. Stated in terms of percentages, leaves 1, 2, and 3 of the dwarfs are 68 percent, 62 percent, and 51 percent, respectively, as long as the comparable leaves of the normals.

Although some of this increase in difference is due to the greater size of successive leaves, allowance was made for this factor. Proportional length increases between leaf 1 and 2 and that between leaves 2 and 3 of the dwarfs were calculated. The theoretical length increase of leaves 2 and 3 of the dwarfs could then be compared with actual measurements. Any decrease of length in the dwarfs below the proportionately expected increase of successive leaves relative to leaf 1, was considered an *extended expression* of d_1. Each of the 31 dwarfs was compared to every normal and the results of these many calculations averaged (Figure 2). The mean *extended expression* was 13.7 mm when comparing measurements of leaves 1 and 2 while the mean *extended expression* between leaves 2 and 3 increased to 21.6 mm. Since the *extended*

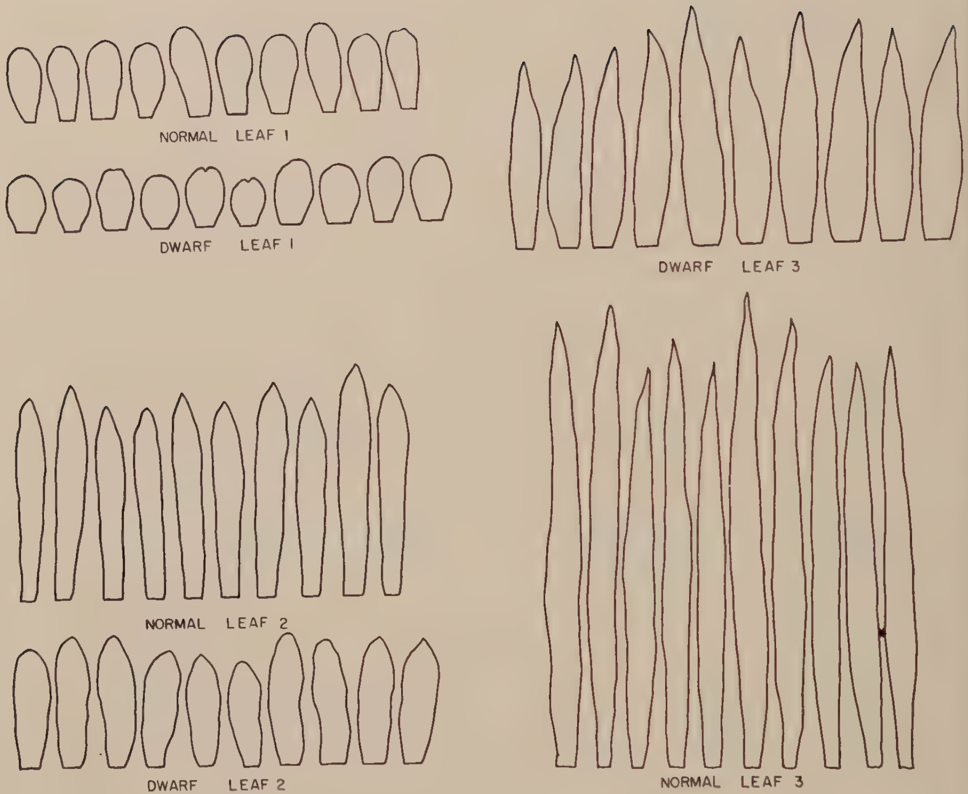

FIGURE 1

Tracings of mature leaves 1 through 3 from 10 dwarf and 10 normal plants.

expression of d_1 in leaves 2 and 3 relative to leaf 1 increases consistently, the trend is one of progressively increasing expression of d_1 in the first three leaves of maize.

Leaf Width. No consistent pattern of measurements such as was found in length seems to be present in the case of leaf width (Table I and Figure 1). In comparing measurements of dwarf and normal phenotypes the expected effect of d_1 is found in the slightly wider leaves of the homozygous recessives. The extent of difference varies, however, as leaf 1 of the dwarfs measures 2.0 mm wider than its normal sibs on the average, while the mean width of leaf 2 in the dwarf is 1.1 mm greater than that of the normals, and leaf 3 dwarfs are 3.8 mm wider than the normals on the average. Thus, the average difference between dwarfs and normals in leaf 2 is slightly less than that of leaf 1, while leaf 3 dwarf and normal differences are greater than those of

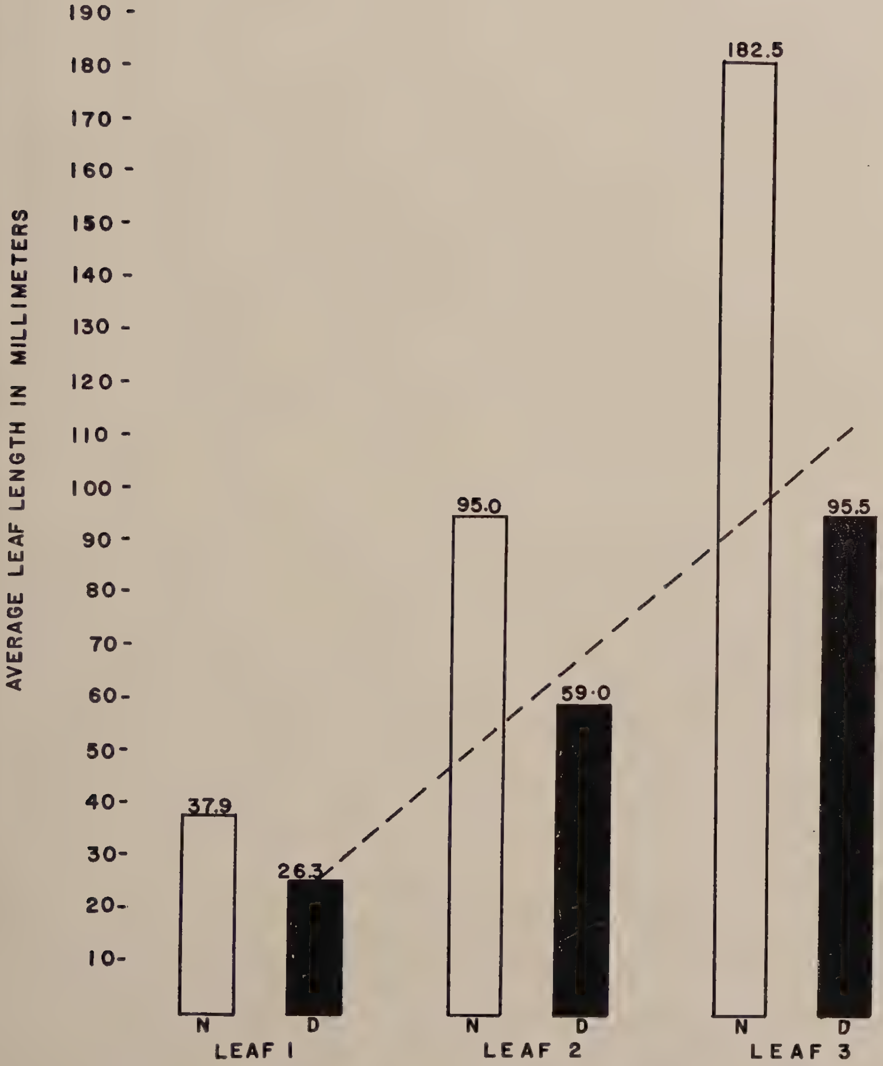

FIGURE 2

Mean length of dwarf and normal leaves 1 through 3. *Extended expression* is shown by the difference between the actual mean of the dwarf as recorded at the top of the bar and the calculated expected proportional increase of successive leaves as represented by the dotted line.

TABLE I

Average length and width of leaves 1 through 3 of dwarf and normal sibs, based on 91 normal and 31 dwarf plants.

LEAF	Leaf Length in Millimeters: Mean and Standard Error	Leaf Length in Millimeters: Difference between means of normal and dwarf plants	Leaf Width in Millimeters: Mean and Standard Error	Leaf Width in Millimeters: Difference between means of normal and dwarf plants
LEAF 1				
normal	37.9± .56	11.6	15.7±.19	2.0
dwarf	26.3± .82		17.7±.21	
LEAF 2				
normal	95.0±1.6	36.0	14.8±.13	1.1
dwarf	59.0±1.8		15.9±.26	
LEAF 3				
normal	182.5±1.6	87.0	14.6±.24	3.8
dwarf	95.5±1.9		18.4±.34	

TABLE II

Maturation dates of length and width of the leaves 1 through 3 of dwarf and normal phenotypes expressed as average days after planting.

LEAF	Leaf length maturity date, in average number of days after planting: Normal	Dwarf	Mean Difference	Leaf width maturity date, in average number of days after planting: Normal	Dwarf	Mean Difference
Leaf 1	8.7	9.1	0.4	8.4	8.7	0.3
Leaf 2	11.4	12.1	0.7	10.8	10.7	0.1
Leaf 3	14.8	16.6	1.8	14.3	14.5	0.2

leaves 1 or 2. Leaf 1 of the normals averages 88 percent as wide as that of the dwarfs, leaf 2 is 93 percent of the dwarfs, while the width of leaf 3 of the normals is 70 percent that of the dwarfs.

Maturation Dates. Table II gives the average maturation dates in length and width of both normal and dwarf plants. Average maturation dates in length show a pattern of increasing difference. Leaf 1 in the dwarfs matures in length 0.4 days later than their normal sibs on the average. Maturity of the dwarfs in length of leaf 2 averages 0.7 days later than its normal sibs. Difference between maturity of dwarf and normal sibs increases to a average of 1.8 days for leaf 3, in which the dwarf is again the slower to mature in length.

On the other hand, maturation dates in leaf width show no consistent trend. Leaf 1 of the dwarfs matures on the average 0.3 day after the leaves of their normal sibs have attained maximum width. In leaf 2 the dwarfs average 0.1 day earlier in width maturity, while in leaf 3 the dwarfs average 0.2 days later than their normal sibs.

DISCUSSION

Although in the present study expression of d_1 is evident in the seedling leaves, no expression of the gene has been observed very early in ontogeny. In the mature embryo normal and dwarf scutella do not differ significantly in their measurements (Pelton 1954). Soon after germination, however, expression of d_1 has been observed in a seedling organ. Hansen and Abbe report that homozygous recessive plants have shorter and wider mesocotyls than do their normal sibs (Hansen 1950, Hansen and Abbe 1943). Shortness of the dwarf mesocotyl is mainly the result of fewer cells having been formed than in its normal sibs. The increased mesocotyl width of the dwarfs as compared to the normals, however, is due to the slightly wider cells of the dwarf mesocotyl.

The present study adds quantitative data on expression of d_1 in the seedling leaves to the above investigations of d_1 in the earlier stages of ontogeny. Although the time of leaf initiation of the dwarf and normal phenotypes was found to be similar in the first three leaves by Stein (1955), these same leaves show phenotypic differences at maturity. Expression of the gene, therefore, has come after leaf initiation. In leaves 1 through 3, as in the later formed leaves, length of the dwarf leaf is less than that of its normal sib while the width of the dwarf leaf is greater than that of the normal.

Analysis of the data on leaf length indicates that expression of d_1 is increasingly greater in the successive seedling leaves. Consecutive leaves of the dwarfs are progressively shorter as compared to their normal sibs. The term *extended expression* is suggested to describe the increased expression of the gene in successive leaves relative to its expression in leaf 1. Although the number of

successive leaves of maize included in this study is too small to come to definite conclusions, the *extended expression* of d_1 seems to consistently increase in the series of leaves measured. That is, there is a progressive expression of d_1 in the three successive leaves. The possibility that this trend is continued in leaves beyond the third is suggested by the study of Phinney (1946) on the eighth leaf of field-grown maize. In this case the eighth dwarf leaf was only 40 percent as long as the eighth leaf of the normal, in contrast with the present study in which the third dwarf leaf was 51 percent as long as the third leaf of the normal. Comparisons with the present study are difficult however, because of the lack of environmental and genetic uniformity between the two investigations.

It is interesting to observe a consistently progressive expression also in the time required for cessation of length growth in the first three leaves. The lack of any consistent trend in leaf width, either from actual measurement or for maturation dates, is puzzling, however, in comparison with the definite trends for leaf length. It therefore seems that in the seedling leaves of maize homozygous for d_1 length of each successive leaf takes progressively more time to attain relatively less growth than in the case of the normal sibs. On the other hand, width of the successive leaves of dwarf plants becomes greater in essentially the same time period required for the normals, and without showing any consistent trend of increasing width.

The relative importance of differential cell division versus cell enlargement in explaining these results is as yet unknown. Hansen and Abbe's work on the mesocotyl (Hansen 1950, Hansen and Abbe 1943) has indicated that reduced length of the dwarf mesocotyl results from a slower rate of cell division, while increased mesocotyl width of the dwarf is a consequence of greater cell enlargement. Whether or not the same pattern occurs in the seedling leaves as occurs in the mesocotyl will require further study. In addition, the physiological basis for the observed changes and the mode of action of d_1 could be probed as in the 1953 Harris work and the current work in the University of California at Los Angeles laboratories of Dr. B. Phinney.

SUMMARY

The expression of a mutant gene, d_1, is analyzed quantitatively for the first three leaves in *Zea mays L.* Maximum length and width as well as dates of maturity of these dimensions in the seedling leaves were recorded for 31 dwarf and 91 normal sibs. Analysis of the data on leaf length shows progressively increasing shortness of successive dwarf leaves as compared to their normal sibs. The expression of the gene d_1 in leaf length is therefore increasingly greater in successive seedling leaves. This progressive trend of gene expression is also present in dates of maturity of leaf length since dwarf leaves mature later in

length than do those of their normal sibs. On the other hand, although the three seedling dwarf leaves all average wider than those of the normals, leaf width does not show a progressive or consistent trend as does leaf length. Nor do maturity dates of leaf width show the consistent trend that is shown by maturation of leaf length.

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A STUDY OF SEED DORMANCY IN EIGHTEEN SPECIES OF HIGH ALTITUDE COLORADO PLANTS

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The investigation reported below involves experimental work dealing with the occurrence and type of seed dormancy exhibited by a number of plants collected at high altitudes in Colorado. The objectives of the work include contributing to an understanding of the autecology of the species studied, as well as aiding in an evaluation of the ecological significance of seed dormancy itself. Collections were made during July and August of 1953 at two localities in Colorado: The Rocky Mountain Biological Laboratory north of Gunnison in the Elk Mountains of south-central Colorado (Gunnison County); and near the former University of Colorado Science Lodge, now the Arctic-Alpine Institute, west of Boulder in the Front Range of Colorado (Boulder County). These localities will be referred to below as R.M.B.L. and Alpine Institute, respectively. The altitudes at which collections were made ranged within what is usually considered to be climatically "subalpine" in Colorado, the lowest collection being at 9200 feet and the highest at 10,000 feet elevation.

The writer wishes to acknowledge the important aid rendered throughout the course of this study both in the field and in the laboratory by his wife, Jeanette S. Pelton. Thanks are also due Dr. William A. Weber, of the University of Colorado, for checking the identifications of the species used, with the exception of *Erythronium grandiflorum*, *Hydrophyllum capitatum*, and *Saxifraga rhomboidea*.

METHODS

Seeds were collected by hand from living plants (not from the ground) at one locality for each species. Dry fruits were shaken in paper bags within one to three days after collection to free the ripe seeds, which were then separated from debris by passing through a series of screens. In this way most of the unripe seeds, which usually were still firmly attached to fruit or inflorescence, were excluded from the material tested. The fleshy fruits of *Sambucus* were crushed and the seeds cleaned by washing through screens; separation by flotation in water was not used since empty as well as filled seeds were desired for viability determinations.

All seeds were air dried and stored in paper envelopes following extraction. Storage temperatures varied for about three weeks after collection, averaging 17°C for the first two weeks (reaching a maximum of 25°C and a minimum

of 7°C); then during transportation from Colorado to Indiana temperatures averaged 27°C for 9 days, reaching an extreme high of 35°C. Subsequently all seeds were stored air-dry in paper envelopes in a constant temperature incubator at 18°C until removed for experimental work.

Germination tests, with exceptions specified under the individual species below, were carried out in Petri dish germinators, with five sheets of filter paper below and two above the seeds, except for the very small seeds of *Saxifraga, Epilobium, Antennaria,* and *Androsace* in which the upper covering of filter paper was omitted. In general, germination tests were performed with duplicate samples of approximately 200 seeds each, cleaned so as to eliminate obviously shrunken or empty seeds (the small seeds under magnification). Caryopses of *Trisetum* were cleaned by eliminating empty florets as seen by transmitted light. De-ionized water was added as necessary to keep the filter paper moist, excess water being carefully drained off. Seeds were considered to have germinated and were removed when the radicle had emerged to a distance equal to the average diameter of the seed. In general, tests were carried out in the dark at a constant 18°C, except where otherwise stated below. This temperature seemed to be satisfactory for many of the species studied, although some of them seemed to have lower optimum temperature requirements and would germinate readily at 8°C in the refrigerator. The scope of the study, however, did not include systematic testing for optimum germination temperatures or other requirements such as light. Special treatments and germination conditions were provided only for those species which would not germinate under the conditions specified above, and these are described below under the particular species to which they apply. Experiments were normally continued until germination had ceased or had dropped to a negligible rate, most of the tests being carried out at least for three to four weeks. The majority of the experiments were completed at Butler University during 1953, 1954, and 1955, but preliminary tests were performed at the Rocky Mountain Biological Laboratory immediately after collection of seed.

At the completion of germination experiments cutting tests were made on the ungerminated seeds, so as to be able to calculate the "real germination percent" (percent germination of normal appearing and filled seeds), as well as the "apparent germination percent" (percent germination of total normal-appearing seeds, both filled and empty).

RESULTS

A summary of the results for each species is presented in Table I. Additional data are provided as follows:

Androsace septentrionalis puberulenta Knuth (202[1]): The highly dormant

[1] Numbers in parentheses refer to the author's voucher collection numbers. With certain exceptions, one set of vouchers has been deposited in the University of Utah herbarium, and a duplicate set retained by the author.

TABLE I

Summary of dormancy and germination tests. Additional data given in text under each species.

Species	Dormancy present or absent	Effective teratment where dormancy present	Real germination percentage[1]
Androsace septentrionalis	present	acid scarification	96.6±1.1
A. parvifolia	absent	no treatment necessary	100.0
Antennaria rosea	"	"	96.3±0.9
Cirsium americanum	weakly present	undetermined	50.0±8.0
Epilobium halleanum	present	embryo excision	61.2±11.5
Erythronium grandiflorum	"	moist-cold stratification	96.6± .8
Galium bifolim	"	acid scarification	98.9± .8
Hydrophyllum capitatum	"	undetermined	negligible
H. fendleri	"	scarification plus stratification	31.5±3.3
Lomatium dissectum	"	moist-cold stratification	47.9±3.3
Mertensia fusiformis	"	undetermined	negligible
Polygonum viviparum	absent	no treatment necessary	100.0
Sambucus microbotrys	present	undetermined	negligible
Saxifraga rhomboidea	"	air-dry 18°C storage	24.9±2.2
Senecio mutabilis	absent	no treatment necessary	99.4± .4
Taraxacum officinale	"	"	100.0
Thlaspi arvense	present	acid scarification	95.0± .6
Trisetum spicatum	absent	no treatment necessary	99.8± .2

[1] Maximum germination obtained from any test, expressed as a percentage of filled and normal-appearing seeds, with the standard deviation of the percentage.

seeds of this species were collected from an open rocky slope at 9,800 feet elevation above the R.M.B.L. on July 27, 1953. Up to 11 months cold-moist stratification at 8°C between moist filter paper in Petri dish germinators was ineffective in breaking dormancy. The only treatment used which resulted in essentially complete germination was concentrated sulfuric acid, indicating the probable cause of dormancy to be an impermeable seed coat. Acid treatment was carried out for 20 minutes, at an average temperature of 24°C. Treated seeds were

washed in running water overnight. Both apparent and real germination were 96.6 ± 1.1[1]%, with a period of 7 days required for the peak rate. Controls showed 39.0 ± 3.0% at the time of the treatment (18 months after collection of seeds), although no germination whatever was obtained from freshly harvested seeds.

Antennaria parvifolia Nutt. (104): Collected August 18, 1953 near the R.M.B.L. on rocky soil in nearly full sun at 9,800 feet altitude. This widely ranging species of open habitats exhibited an apparent germination of 64.4 ± 2.4% and a real germination of 100.0% without treatments, requiring 6 days to reach a peak germination.

Antennaria rosea Greene (103): Abundant on an open cut-over knoll in shallow gravelly soil near the Alpine Institute at 9,800 feet elevation. Collected August 17, 1953. Apparent germination without treatment was 94.2 ± 1.2%, and real germination 96.3 ± 0.9%. Fifteen days were necessary for the peak germination rate to be attained. Germination in this species was atypical in that the radicle emerged after the hypocotyl and epicotyl.

Cirsium americanum (Gray) Robbins. (112): Collected from an open dry meadow above the Alpine Institute at 10,000 feet elevation on August 17, 1953. The heads of this species were heavily infested with larvae, and even the remaining achenes exhibited low viability. Apparent germination without treatment was only 5.0 ± 3.4%, and real germination 50.0 ± 8.0%, the peak being reached in 8 days. Insufficient numbers of viable seeds of this species were obtained to investigate the apparent weak dormancy further.

Epilobium halleanum Hausskn. (200): Seeds of this species were collected on August 4, 1953 above the R.M.B.L. at 9,800 feet elevation, along a dry creek bed in part shade of aspens. Very poor germination was obtained under most of the treatments used, although cutting tests indicated a high viability (over 93%). Eleven months of cold-moist (8°C) stratification resulted in 1.4 ± .4% apparent germination and 1.5 ± .5% real germination upon removal to 18°C. Eighteen months air-dry 18°C storage gave 1.5 ± .4% apparent germination in diffuse light, although when freshly collected no results were forthcoming. Hot water treatments, and pot tests in soil left outdoors overwinter or subjected to combinations of greenhouse and refrigerator temperatures were unsuccessful. Scarification and embryo excision tests strongly suggest that a seed-coat imposed dormancy is present, although sulfuric acid treatment proved impractical because of the minute size of the seeds. In one test seed coats were shaved off one edge of fifty seeds with a sharp razor and 26.5 ±

[1] Standard deviation of the percentage, from the formula $\sigma = \sqrt{\frac{p(1-p)}{N}}$, where p is the germination percentage obtained represented as a decimal and N is the number of seeds upon which the percentage is based.

11.5% developed into seedlings. The remainder of the embryos molded, suggesting that perhaps the real germination was much higher. Only 0.6 ± .6% of the control seeds germinated in this test. In another test, the embryos were excised from eighteen seeds, of which 61.2 ± 11.5% dveloped into seedlings on filter paper in the dark.

Erythronium grandiflorum ssp *chrysandrum* Pursh. Seeds were collected at 9,800 feet from plants along edges of a dry creek bed in partial shade near the R.M.B.L., on August 4, 1953. A moist-cold stratification between moist filter paper in Petri dishes was found to be sufficient to break the profound dormancy of the species. During five months storage under these conditions, 96.0 ± .9% apparent germination and 96.6 ± .8% real germination was obtained without transfer to higher temperatures (all germination occurred at 8°C). One hundred days were required to reach the peak germination at this low temperature. Freshly harvested and 18 month old controls gave no results.

Galium bifolium Wats (109): An abundant species in partial shade at 9600 feet elevation above the R.M.B.L., collected July 15, 1953. No germination was obtained without treatments, but eleven months cold-moist (8°C) storage yielded only 1.4 ± .7% apparent and real germination. Concentrated sulfuric acid for 27 minutes at an average temperature of 27°C was highly successful, however, giving 81.0 ± 3.0% apparent germination and 98.9 ± .8% real germination, as tested on January 5, 1955. Most of the germination occurred at 8°C rather than the 18°C normally used in the test, requiring 6 weeks to reach a peak. Two hundred seeds planted on November 30, 1954, in loam soil in pots and sunken in the soil outdoors gave essentially 100% germination by April 14 in Indianapolis. It is probable that in this case the action of fungi on the seed coat over the winter permitted the seeds to germinate, since the laboratory tests indicated an impermeable seed coat was involved rather than physiological requirement for a cold treatment. No germination was obtained from either freshly harvested or 18 month old seeds in control runs.

Hydrophyllum capitatum Doug. ex Benth. (250): This is a common early flowering plant collected in part shade of aspens above the R.M.B.L. at 9,800 feet. Seeds were obtained on August 4, 1953, and showed a profound dormancy. Although the seeds exhibited a high viability (92%), only relatively small quantities were extracted and so most of the tests of this species were carried out with half the number of seeds used for the other species. Moist-cold stratification for eleven months gave only 2.7 ± 2.1% apparent germination and 2.8 ± 2.2% real germination and none for the controls. No other treatments were successful for the species, including higher germination temperatures, light treatments, soil tests, sulfuric acid treatment, mechanical scarification, hot water, and combinations of scarification and stratification.

Hydrophyllum fendleri (Gray) Heller (101): Locally abundant along a

stream near the Alpine Institute at 9,500 feet altitude, collected on August 18, 1953. During eleven months cold-moist stratification an apparent germination of 8.6 ± 1.2% and a real germination of 10.2 ± 1.4% were obtained. Controls using either freshly harvested or 18 month old seeds gave no results. Single treatments using sulfuric acid, hot water, and scarification were also unsuccessful. Soil tests, however, in which the seeds were in moist loam at greenhouse temperatures for 6½ weeks and then under moist-cold stratification temperatures (8°C) for 5 months yielded 31.5 ± 3.3% apparent germination. In this case apparent germination closely approximates the real germination percent since sample cutting tests of other seeds from the same lot indicated essentially full viability. Much poorer germination (5.5 ± 1.6%) was obtained from soil tests in which the seeds were in the greenhouse for 13 weeks but at stratification temperatures for only three months. Most germination occurred at 18°C (once dormancy had been broken), but some seeds germinated at 8°C.

Lomatium dissectum multifidum (Nutt.) Math. and Const. (110): Material of this species was obtained at 9,600 feet elevation, near the R.M.B.L. on July 27, 1953, where it is locally abundant on dry rocky slopes. During eleven months at 8°C cold-moist stratification an apparent germination of 40.5 ± 3.2% and a real germination of 47.9 ± 3.3% was obtained with the highly dormant mericarps, a peak not being obtained until 11 months. Germination occurred both at 8°C and subsequently when transferred to 18°C. No germination occurred in either fresh or 18 month old control tests. Several other treatments, including mechanical and chemical scarification, hot-water, and pot plantings in soil left outdoors overwinter were also tried. Of these the outdoor pot cultures yielded the only germination, but this was appreciably lower than the Petri-dish tests, reaching a real germination of only 25.0 ± 3.1%. No results were obtained from pot cultures kept for 6 to 13 weeks in the greenhouse followed by 3 to 5 months at 8°C stratification.

Mertensia fusiformis Greene (120). Collected on July 7, 1953 from 9,800 feet elevation above the R.M.B.L. where the species is a frequent early flowering species in open and semiopen fairly dry sites. After eleven months of moist-cold stratification this dormant-seeded species yielded 4.7 ± 1.3% apparent germination and 11.6 ± 2.0% real germination. Nicking of the seed coat, embryo excision, hot water, sulfuric acid treatment or soil tests did not improve germination appreciably, nor did up to eighteen months of dry storage of 18°C.

Polygonum viviparum L. (108): Locally abundant along a stream in moderate shade above the Alpine Institute at 10,000 feet elevation, where it was collected on August 17, 1953. This species bears bulblets as well as seeds in the inflorescence, but insufficient quantities of the bulblets were collected for testing. Apparent germination of seeds without treatment was 84.7 ± 1.5%, and real germination 100.0%, peak germination being reached in 7 days.

Sambucus microbotrys Rydb. (102): Common along streams near the Alpine Institute at 9,500 feet altitude. Collected August 18, 1953, at a stage when most of the fruits were either yellow or red in color. The profound dormancy was not appreciably affected by moist-cold stratification for eleven months (0.5 ± .36% apparent germination and 1.0 ± 5% real germination). Neither were scarification, hot water, soil cultures, or sulfuric acid treatments effective by themselves.

Saxifraga rhomboidea Greene. A locally common species collected on July 22, 1953 above the R.M.B.L. at 9,800 feet elevation on rather dry rocky soil in nearly full sun. Although freshly harvested seeds were highly dormant, this seems to gradually lessen with age, regardless of storage conditions. After 18 months of air-dry storage at 18°C, an apparent germination of 21.2 ± 2.1% and a real germination of 24.9 ± 2.2% was obtained with a peak at 14 days at 18°C in the dark. Somewhat lower percentages were obtained after eleven months of moist-cold stratification. Hot water treatments, mechanical scarification, germination in diffuse light instead of darkness, and pot tests in soil subjected to various combinations of treatment, including outdoors overwinter, were not successful in hastening the breaking of dormancy in these seeds.

Senecio mutabilis Greene (106): Locally frequent on an open rocky slope above the R.M.B.L. at 9,700 feet. Apparent germination without treatment was 85.6 ± 1.7%, and real germination 99.4 ± .4%, with a peak at 6 days.

Taraxacum officinale Web. (111): This cosmopolitan species is very abundant in open dry meadows. Seeds were collected from the grounds of the R.M.B.L. at 9,500 feet on July 11, 1953. Apparent germination was 94.9 ± .9% and real germination 100.0%. Peak germination was reached in 7 days.

Thlaspi arvense L. (201): This widely spread adventive species is only locally abundant in the vicinity where collected, at 9,200 feet altitude a few miles south of the R.M.B.L. on a dry road cut. The very dormant seeds were obtained on July 27, 1953. Treatment of seeds by cold-moist stratification at 8°C for eleven months resulted in only 0.51± .4% apparent and real germination. Eleven minutes of concentrated sulfuric acid at 32°C, however, gave 68.3 ± 1.3% apparent germination, and 95.0 ± .6% real germination, requiring seven days to reach a peak. Control tests immediately after harvest, and also after 18 months air-dry storage gave no germination at all. Seeds planted in soil in pots left outdoors overwinter gave 41.5 ± 3.6% germination, perhaps as a result of the breakdown of the seed coats by fungal action.

Trisetum spicatum Richt. (105): Collected on August 18, 1953 in an open grassy meadow at 2,700 feet elevation, above the Alpine Institute. Apparent germination without treatments, based on caryopses which appeared filled by transmitted light, was 98.7 ± .6%, and real germination 99.8 ± .2%. Appar-

ent germination based upon seemingly sound fruits not selected with the aid of transmitted light, however, was only 52.4 ± 2.5%, since a large proportion of the caryopses were empty. Peak germination was reached in 14 days.

DISCUSSION

The eighteen species here reported upon can be tentatively classified according to the type of dormancy exhibited as follows:

A. Seeds lacking dormancy and germinating readily in a favorable environment: *Antennaria parvifolia, A. rosea, Cirsium americanum* (partially dormant), *Polygonum viviparum, Senecio mutabilis, Taraxacum officinalis,* and *Trisetum spicatum.* As is frequently the case, the composites and the one grass fall into this category.

B. Seeds possessing a dormancy largely satisfied by a scarification treatment, by acid or mechanical means: *Androsace septentrionalis puberulenta, Epilobium halleanum, Galium bifolium,* and *Thlaspi arvense.* It has not yet been determined whether the inhibition, apparently caused by the seed coat, is a result of impermeability to water or gases, to mechincal restriction, to chemical inhibitors, or other causes.

C. Seeds requiring only prolonged stratification under moist cold conditions to break their dormancy: *Erythronium grandiflorum* ssp *chrysandrum,* and *Lomatium dissectum multifidum* (partially effective). The physiological processes occurring during such a period may vary with the species, and therefore this type of dormancy can be caused by several mechanisms (Crocker and Barton 1953).

D. Seeds showing other types of dormancy, such as combined seed coat inhibition and dormant embryos, or dormancy mechanism undetermined: *Saxifraga rhomboidea, Hydrophyllum capitatum, H. fendleri, Mertensia fusiformis,* and *Sambucus microbotrys.*

Where dormancy seems to be present it may eventually be shown that the requirements for germination were not satisfied, and therefore the above classification is strictly tentative.

The results for *Thlaspi* are somewhat at variance with those of Bibbey (1948) who concluded that an overwinter stratification was necessary to break dormancy. In the present series of experiments outdoor plantings did yield up to 42 percent germination, although a moist-cold stratification between filter paper was ineffective by itself. Acid scarification yielded up to 95 percent germination, however, without any stratification treatment. It therefore seems likely that outdoor stratification in soil permits fungi to break down the seed coats sufficiently to permit fair germination the following spring.

The type of dormancy shown by *Saxifraga rhomboidea* is puzzling, since a time factor seems to be the limiting feature. What the morphological or physiological processes are that eventually permit germination to occur have not been determined. On the other hand, several species of *Saxifraga* studied by Webb (1950) show no dormancy at all.

In the case of *Sambucus microbotrys* preliminary experiments suggested that acid scarification followed by moist-cold stratification might yield positive results. A combination seed coat and embryo dormancy would be expected if this species follows the pattern of those members of the genus previously tested (U.S. Forest Service, 1948), although treatments similar to those recommended by this publication were not found to be effective with *S. microbotrys*.

Hydrophyllum capitatum shows profound dormancy probably of a complex nature. Very possibly a combined seed coat and embryo dormancy is present, and that seed coat scarification or decay followed by moist-cold stratification is necessary to break the dormancy. Up to 13 weeks in moist loam soil at greenhouse temperatures, however, followed by three months at 8°C, had no effect.

The results suggest that in *H. fendleri* a strong embryo dormancy requiring moist-cold stratification is present but that a lesser seed coat inhibition must first be removed. The period of time in soil at greenhouse temperatures was probably sufficient to remove this seed coat restriction through fungal activity, thus permitting subsequent after-ripening of the embryo under conditions of stratification. In these tests the seeds produced extensive roots but the epicotyl did not emerge before termination of the experiment. There may be, therefore, an epicotyl dormancy in this species, but this possibility was not investigated. Very likely both a seed coat inhibition and an embryo dormancy are present also in *Mertensia fusiformis*, although the solution of the problem requires additional experimental work.

The adaptational significance of seed dormancy as a mechanism causing germination to occur at a time or place favorable to the subsequent survival of the seedlings is reasonably well established for certain well-studied plants. Precisely to what extent, however, the occurrence, depth, and mechanism of dormancy of seeds is related to environmental necessities is uncertain for the vast majority of species. In a study of a very large number of California plants, Mirov (1936) has shown significant correlations between the occurrence and type of seed dormancy with altitudinal zone. It was found that at higher elevations a greater proportion of the plants required cold-moist stratification than at lower elevations, but that at any given altitude dormancy may be either present or absent, and if present of several possible types.

Even in the relatively small sample of species reported in the present paper, however, it is apparent that the same climatic condition does not necessarily result in the development of parallel seed behavior; several species show no

seed dormancy at all, while of the dormant types several mechanisms insuring delayed germination are involved in the different species. This variability in the occurrence of dormancy in different species even under nearly identical climatic conditions does not nullify the possible adaptive value of seed dormancy. The significance of any plant character or process must be viewed in the context of the entire life cycle. In one species the reproductive habits may be so adjusted that delayed germination owing to dormancy may be disadvantageous, whereas another species in the same habitat may require postponement of germination to a subsequent season for satisfactory survival of seedlings. Nevertheless, it may be expected that a given habitat may evoke the evolution of one type of seed behavior more frequently than the same habitat results in the development of other types, and it is for this reason that correlations such as those obtained by Mirov are so strongly suggestive. We may expect that the ecological and evolutionary significance of seed dormancy will be much better understood as its occurrence and mechanisms gradually become better known.

SUMMARY

A study of the occurrence and type of seed dormancy in eighteen species of plants collected in two high altitude regions of Colorado gave the following results:

Seeds lacking dormancy: (1) *Antennaria parvifolia* Nutt. (2) *Antennaria rosea* Greene (3) *Cirsium americanum* (Gray) Robins. (partially dormant) (4) *Polygonum viviparum* L. (5) *Senecio mutabilis* Greene (6) *Taraxacum officinalis* Web., and (7) *Trisetum spicatum* Richt.

Seeds possessing a dormancy requiring seed coat scarification only (by acid or mechanical treatments): (1) *Androsace septentrionalis puberulenta* Knuth (2) *Epilobium halleanum* Hausskn. (embryo excision most effective) (3) *Galium bifolium* Wats, and (4) *Thlaspi arvense* L.

Seeds requiring moist-cold stratification only: (1) *Erythronium grandiflorum* ssp *chrysandrum* Pursh., and (2) *Lomatium dissectum multifidum* (Nutt.) Math. and Const. (partially effective).

Seeds showing other types of dormancy: (1) *Saxifraga rhomboidea* Greene exhibits a dormancy which gradually lessens with age in dry 18°C storage, but has not been successfully broken by any treatments so far attempted. (2) *Hydrophyllum capitatum* Doug. ex Benth., (3) *Hydrophyllum fendleri* (Gray) Heller, (4) *Mertensia fusiformis* Greene, and (5) *Sambucus microbotrys* Rydb. all seem to have a double dormancy involving both seed coat and embryo or other conditions, but will require further investigation.

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FOREST COMMUNITIES IN VERSAILLES STATE PARK, INDIANA[1]

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Continuity of observation over an extended period of time is a difficult but vital phase of the study of the natural vegetation of any area. Such continuity is difficult to obtain. The vegetation may be destroyed or the investigator may move before sufficient time has elapsed to permit any significant development. Dr. J. E. Potzger realized the difficulties inherent in a long-time study but he also considered such studies valuable. Hence in 1950 he and Mrs. Potzger published the results of their studies on several areas in Versailles State Park. These were planned as the ground work for a long-time study of succession.

This paper supplements the original observations with data obtained by a different method. It is to be hoped that this long-time study will be continued and extended. The increased quantitative background presented here should clarify changes as they become apparent in the future.

GEOGRAPHY AND PHYSIOGRAPHY

Versailles State Park in Ripley County, Indiana lies in the Illinoian Till Plain region often called the "Flats." This is an extensive area of poorly drained, severely leached soils, chiefly silt loams and clay loams underlain in many places by clay pan. In the region of the park Laughery Creek and its tributaries have cut deep valleys and ravines into the plateau thus providing a variety of slope gradients and exposures and improving the natural drainage of much of the area.

Prior to establishment of the park most of the forested areas were subjected to severe cutting and some of the land was under cultivation. Thus the vegetation now present shows a wide variety of successional communities as well as numerous physiographic segregates. This area lies within the Western Mesophytic Forest region as described by Braun (1950).

METHODS

Field data were obtained by means of the random pairs method (Cottam and Curtis, 1949) which is based on the sampling of a pair of trees at each of many randomly selected points. The method has an advantage over the quadrat method

[1]This is paper 6 of the Conservation Education Camp faculty.

in that it provides a large number of sample units with a relatively small expenditure of time and labor. In this study an exclusion angle of 180° was used and a correction factor was applied (Cottam and Curtis, 1955). Four stands were chosen to represent different topographic and historic patterns. A total of 70 points were established and 140 trees measured and recorded in stands 1, 2 and 3 and 140 points were established and 280 trees recorded in stand 4. All stems 4 inches or over d.b.h. were recorded as trees. Stems over 4 feet in height but under 4 inches d.b.h. were recorded in 6 foot wide transects between each sample pair of trees. These stems were classed as reproduction. Tree seedlings and herbaceous species were not studied in detail.

Frequency, relative density and basal area were determined for each species in each stand and the number of trees per acre was calculated. The expressions of frequency and relative density are used as defined by Curtis and McIntosh (1950). The importance value for each species was also determined by summing the frequency, relative density and per cent basal area values for that species. Field sampling was accomplished in June of 1955 by students of the Conservation Education Camp with the assistance of Mr. A. N. Liming, District Forester, Professor Howard Michaud, Director of the Conservation Education Camp, and the author. Nomenclature follows that of *Trees of Indiana* (Deam and Shaw, 1953).

RESULTS AND DISCUSSION

The primary characteristics of the four stands studied are shown in Table I. Stands 1 and 2 are on the poorly drained flats and are essentially the same as the two areas examined by Dr. Potzger and Mrs. Potzger in their study of secondary succession on the Illinoian Tillplain (1950). Stand 3 covers the upper portion of a well-drained southwest-facing slope near the Conservation Education Camp, and overlaps an area described by Dr. Potzger (see table 1, Potzger, 1950) in his work on forest types in Versailles State Park. Stand 4 is a relatively undisturbed old-growth stand described in table 2 of the same paper.

An examination of the diameter class data presented by Dr. Potzger indicates that no drastic change has taken place in the composition of the four stands. However, after only eight years, some indication of future change is available and this will be discussed in reference to individual stands. The similarity of results obtained by the random pairs method with that from the quadrat method used by Dr. Potzger validates the use of the more rapid method in this vegetational area.

TABLE I

Characteristics of four forest communities in Versailles State Park

	Dominant species	Number of Trees per Acre	Basal Area per Acre, sq. ft.	Tree species present
Stand 1. Young stand "Flats" type Poorly drained.	Acer rubrum Liquidambar styaciflua	67	9.9	10
Stand 2. Older stand "Flats" type.	Acer rubrum Fagus grandifolia Quercus alba Carya ovata	236	191.8	16
Stand 3. Mixed hardwood on south-west slope.	Acer saccharum Quercus rubra Carya cordifomis Carya glabra	191	101.1	22
Stand 4. Oldgrowth forest on level well drained residual soil.	Acer saccharum Fagus grandifolia	122	160.4	18

TABLE II

Composition of a young forest community on the "flats" (Stand 1)

Species	Frequency	Relative Density	% Basal Area	Importance Value	% Reproduction
Liquidambar styraciflua	78.6	62.0	56.0	196.6	29.5
Acer rubrum	34.3	19.3	19.5	73.1	20.5
Robinia pseudoacacia	12.8	7.9	11.3	32.0	19.6
Prunus serotina	7.2	3.5	6.3	17.0	3
Platanus occidentalis	4.3	2.1	2.5	8.9	1.5
Liriodendron tulipifera	4.3	2.1	2.3	8.7	2.4
Juniperus virginiana	2.9	1.4	1.4	5.7	3.5
Fraxinus americana	1.4	.7	.4	2.5	2.0
Nyssa sylvatica	1.4	.7	.4	2.5	1.5

TABLE III

Change in stem size in a young forest community (Stand 1) on the "Flats"[1] shown by number of trees in each size class

Species	Year	Size Class 1-2 inches[2]	3-5 inches	6-10 inches	Total stems
Liquidambar styraciflua	1948	384	45	—	429
	1955	158	70	17	245
Acer rubrum	1948	409	4	1	414
	1955	110	21	6	137
Robinia pseudo-acacia	1948	4	—	—	4
	1955	105	6	5	116
Prunus serotina	1948	10	—	—	10
	1955	16	1	4	21
Platanus occidentalis	1948	11	1	—	12
	1955	8	1	2	11
Liriodendron tulipifera	1948	40	1	—	41
	1955	13	2	1	16

1. 1948 data from Table 3, Potzger 1950.

2. Includes all stems classed as reproduction in the 1955 study, i.e. under 4 inches d.b.h. and over 4 feet tall, and all stems included in the under 1 inch and 1-2 inch classes in the 1948 study.

Stand 1

As indicated in Tables I and II, stand 1 is a relatively open stand dominated by sweet gum and red maple with an intermixture of other intolerant pioneer species. The area had originally been under cultivation and was abandoned about 1930. The soil is Clermont silt loam, very poorly drained, acid and infertile, and supports a preponderance of the herbaceous plants common to such a habitat including *Plantago artistata, Antennaria spp., Rubus spp.* and *Andropogon virginicus*. Black locust has been planted in the area and is now a minor component of the vegetation. The soil has only a slight accumulation of humus and lichens are abundant as ground cover in the open areas. Comparison of the data with those obtained by Dr. Potzger in 1948 (Potzger, 1950) indicates virtually no change in the species composition of the stand. There has been a considerable shift in size distribution (Table III) indicating that growth conditions have been relatively favorable in the intervening years despite the drouthy summers of 1953 and 1954. Oaks continue to be missing from the stand, in all probability because seed is not readily available anywhere save on the fringe of the stand where it joins the older forest.

TABLE IV

Composition of older forest community on "Flats" (Stand 2)

Species	Frequency	Relative Density	% Basal Area	Importance Value	% Reproduction
Fagus grandifolia	33	18.5	36.1	87.6	17.3
Acer rubrum	33	21.4	12.7	67.1	6.5
Quercus alba	18.6	10.7	16.6	45.9	5.0
Carya ovata	18.6	10.0	4.8	33.4	12.9
Liquidambar styraciflua	11.4	6.4	6.8	24.6	1.4
Liriodendron tulipifera	14.3	6.4	4.0	24.7	0.7
Sassafras albidum	14.3	6.4	1.9	22.6	15.1
Quercus rubra	11.4	5.7	4.2	21.3	5.7
Nyssa sylvatica	5.7	3.6	5.7	15.0	2.2
Fraxinus americana	5.7	2.9	2.2	10.8	12.2
Acer saccharum	4.3	2.9	0.8	8.0	0
Ulmus americana	4.3	2.1	0.6	7.0	2.2
Quercus muhlenbergii	1.4	.7	2.2	4.3	0
Tilia americana	1.4	.7	0.6	2.7	1.4
Ulmus rubra	1.4	.7	0.2	2.3	1.4
Carpinus caroliniana	1.4	.7	0.1	2.2	0.7

Stand 2

In stand 2 drainage and soil conditions closely approximate those in stand 1. Lacking prior cultivation the soil structure is somewhat better than in stand 1 and in addition there are numerous inconspicuous small hummocks resulting from windfalls. The dominant species of the community are beech, red maple, white oak and shagbark hickory (Table IV). This stand had been subjected to some cutting and other disturbance prior to 1930. The presence of a few old oak stumps almost 30 inches in diameter is evidence that oak was once a stronger component of the stand. The stand is so dense, with 236 stems over 4 inches d.b.h. per acre, that little light penetrates the canopy. The floor of the forest is open with only a sparse herbaceous cover and few shrubs. A thick layer of leaf mould and litter has developed on the soil surface.

The total basal area of trees of this community is larger than that found in any of the other three stands (Table I). Even so there are few trees over

TABLE V

Stem size is a well-established forest community on the "flats"[1] as indicated by number of trees in each size class (Stand 2).

Species	Year	Size Class 0-2 in.[2]	3-5 in.	6-8 in.	9-15 in.	16-20 in.	over 20 in.	Total stems
Fagus grandifolia	1948	72	18	2			3	95
	1955	24	7	2	5	3	9	50
Acer rubrum	1948	32	24	16	16	4	1	93
	1955	9	6	9	14	1		39
Quercus alba	1948	16	7	3	3		1	30
	1955	7		5	6	1	3	22
Carya ovata	1948	45	8	2	2			57
	1955	18	6	2	5			31
Liquidambar styraciflua	1948	4	9	5	5	4		27
	1955	2	2	1	5	3		13
Liriodendron tulipifera	1948	1	1	1	1	1		5
	1955	1		5	4			10
Sassafras albidum	1948	1	8	11	1			21
	1955	21	3	5	1			30
Quercus rubra	1948	9	4	2	6	1		22
	1955	8	1	2	5			16

1. 1948 Data taken from Table I Potzger and Potzger, 1950
2. Includes all stems classed as reproduction in this study and in the 1948 study. (i.e. under 4 inches d.b.h. and over 4 feet tall).

20 inches d.b.h. A check of the diameter distribution of stems in both the 1955 and the 1948 (Potzger and Potzger, 1950) data shown in Table V indicates that there are probably two major age groups present in the beech and the white oak. No explanation is immediately available for this particular condition. Oaks have been shown to be major components of most stands found on the "flats" (Potzger and Liming, 1953). The major problem seems to be to determine the time and mode of invasion of oaks into communities such as stand 1 which at approximately 25 years after abandonment still is devoid of oak.

Dr. Potzger had suggested that, "If the oaks and beech are prevented for another 10 to 15 years from invading the area removed 300 feet from the mature forest it appears likely that sweet gum, red maple and tulip poplar will have formed a closed crown cover under which invasion may be impossible. Here would then develop a different forest cover type than in the area which is

TABLE VI

Composition of a forest community on a south facing slope (Stand 3).

Species	Frequency	Relative Density	% Basal Area	Importance Value	% Reproduction
Quercus rubra	27	17.1	31.9	76.0	5.6
Acer saccharum	36	18.6	6.4	61.0	35.2
Carya glabra	23	14.3	14.8	52.1	6.4
Carya cordiformis	20	12	9.6	41.6	0.8
Ulmus rubra	18.5	10	7.3	35.8	4.8
Fraxinus americana	11.5	5.7	5.6	22.8	13.6
Quercus muhlenbergii	10	5.0	6.9	21.9	4.8
Prunus serotina	7.1	3.6	4.0	14.7	
Ulmus americana	7.1	3.6	1.4	12.1	1.6
Juglans nigra	2.9	1.4	2.5	6.8	
Acer rubrum	2.9	1.4	1.6	5.9	3.2
Sassafras albidum	2.9	1.4	1.4	5.7	1.6
Tilia americana	2.9	1.4	1.3	5.6	8.8

a few feet closer to the source of seed dissemination, even though habitat conditions otherwise would be alike." (Potzger and Potzger, 1950). However, crown cover is not closing as rapidly as might be expected and it may be that the process will extend over a period of 30 to 50 years. In this event there is still ample opportunity for invasion by oaks and other species in the openings between thickets of gum and maple. In this respect also Chapman (1942) has stated, "It is recognized that the composition of the forest stand does not vary greatly from that of the established seedling stand during many years of subsequent development; that is, the crucial period in composition determination is during the early seedling stages. The relation between seedlings and their environment is often undervalued as a determinant of the species composition of forest stands."

He also says that "In the central hardwood region, where a wealth of species is found, the influence upon forest composition of changes of even a few inches of elevation is expressed clearly on poorly drained flat lands, and may be observed also on areas of greater relief."

TABLE VII

Composition of an old-growth forest community on well drained soil (Stand 4)

Species	Frequency	Relative Density	% Basal Area	Importance Value	% Reproduction
Fagus grandifolia	42	27.5	60.1	129.6	2.2
Acer saccharum	55	33.9	15	103.9	65.0
Fraxinus americana	14.3	7.1	3.5	24.9	1.3
Nyssa sylvatica	8.5	4.6	5.4	18.5	1.1
Juglans nigra	9.3	4.6	3.8	17.7	1.3
Cornus florida	8.6	5.0	0.6	14.2	7.1
Liriodendron tulipifera	3.5	1.8	2.2	7.5	0.7
Prunus serotina	4.2	2.1	1.2	7.5	1.1
Carya ovata	4.3	2.4	0.7	7.4	1.3
Ulmus rubra	4.3	2.1	0.7	7.1	1.8
Tilia americana	3.5	2.1	1.6	7.2	0.2
Quercus rubra	3.5	1.8	1.7	7.0	0.2
Quercus alba	2.1	1.1	0.6	3.8	
Celtis occidentalis	2.1	1.1	2.0	5.2	1.1
Ostrya virginiana	1.4	.7	0.08	2.2	1.3

Obviously several lines of investigation are indicated if the position of the component species in the stand is to be properly evaluated. Investigation is needed on seedling requirements and on the site preferences of saplings and mature trees. The long range study initiated by Dr. Potzger will make it possible to note actual changes as they occur.

Stand 3

This forest community lies on the upper portion of a long south slope just east of the Conservation Education Camp. The soil, classed as Switzerland, is residual material derived from the underlying shales and limestone and has good surface drainage and aeration. The forest is a mixed mesophytic type community with a variety of species sharing the dominant position. The composition of the stand is shown in Table VI. Windfall, disease and other natural catastrophe will probably provide sufficient openings to maintain the mixed character of the stand although the bulk of the reproduction is sugar maple. The ground cover includes many herbaceous species and the shrub layer is more

varied and conspicuous than in stand 2. There has been very little disturbance in the stand for many years although it was once partly lumbered. The lower and steeper portion of this slope not sampled in this study is considerably more xeric and with a much greater abundance of oak. Shifts in the relative importance of sugar maple and white ash on the one hand and red oak and the hickories on the other will probably occur but it is too early to predict the final outcome in stand composition.

Stand 4

Stand 4, located on residual soils in the southeastern portion of the park, is an old-growth stand which has not been recently subjected to appreciable disturbance. It is primarily a beech and sugar maple community with a considerable admixture of other species as indicated in Table VII. The area slopes slightly toward a small stream that winds along the edge of the community. Nowhere is the surface flat and without adequate drainage. Although beech is a major dominant the community is obviously different from those found on the "flats" in that the associated species are different (Braun, 1953) and the presence of sugar maple in particular is evidence of lower acidity and better drainage.

Large stems of sassafras, black cherry and other species indicate that some factor caused the stand to be opened-up considerably, probably between 100 and 200 years ago. The extremely high percentage of maple reproduction has been noted by other authors and does not mean that sugar maple will eventually be the sole dominant. Many of the beech trees are of great size and have reached the point where windthrow or death of a single individual will influence a considerable area of the community. Thus within a relatively few years it will probably be possible to observe some shifts taking place in composition.

SUMMARY

Four different forest communities in Versailles State Park were studied using the random pairs method of sampling.

These include a young and an older community on the poorly drained Illinoian till, a well developed mixed-mesophytic community on sloping residual soils and an old-growth beech and sugar maple community on level well drained residual soils.

The young stand on the "flats" is open and is composed primarily of red maple and sweet gum. The older stand on the "flats" is dominated by a mixture of beech, red maple, white oak and shagbark hickory in a dense stand. The community on the south slope included 22 different arboreal species among which sugar maple, red oak, bitternut hickory and pignut hickory have the

highest importance values. The old-growth beech and sugar maple community appears closer in type to the beech-maple forests north and east than to the mixed mesophytic or the "flats" type of community.

Data are presented to add to that already available so that in the future periodic studies can be made to follow the development of communities of various ages and composition in this area.

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THE FOREST PRIMEVAL OF INDIANA AS RECORDED IN THE ORIGINAL U. S. LAND SURVEYS AND AN EVALUATION OF PREVIOUS INTERPRETATIONS OF INDIANA VEGETATION

JOHN E. POTZGER[1], MARGARET ESTHER POTZGER[2], and JACK McCORMICK[3]

Between 1799 and 1846, the territory which now comprises the State of Indiana was divided by the United States public land survey into six-mile-square townships as a prerequisite for the equitable distribution of public lands. Each township, in turn, was subdivided into 36 sections one-mile square. Section and quarter-section corners, as well as a number of intermediate points, were marked by blazing trees. The location, name, and diameter of more than 214,-500 "witness trees," composed of more than 80 species and generic groups, were recorded in the Indiana surveyors' journals. These journals and the maps compiled from them, records inscribed before a tidal wave of settlers swept away much of the natural vegetation of the State, represent our most tangible account of Indiana's primeval forests. They are the source of data for this study.

PREVIOUS STUDIES BASED UPON SURVEY DATA

Six detailed studies which have drawn upon small segments of the Indiana records of the United States public land survey have been published (Blewett and Potzger 1950, Rohr and Potzger 1950, Potzger and Potzger 1950, Ross 1950, Finley and Potzger 1952, Potzger and Keller 1952). A seventh is in preparation (McCormick mss.). The object of the present paper is to present an over-all picture of the original forest vegetation of Indiana.

In their study of the forest associations of Marion and Johnson Counties, neighboring agricultural counties in the glaciated central part of the State, Blewett and Potzger (1950) found that, "*Fagus grandifolia* and *Acer saccharum* combined constituted one-half or more of the stems in all but five of the 28 townships [in the two counties], and *Fagus* alone has 50 per cent representation or more in most of them, reaching a maximum of sixty-nine per cent . . . Combining hickory with oaks as an ecological group, their maximum representation (Marion County) is 19 per cent . . ., but in most townships it does not exceed ten per cent."

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[1]Dr. Potzger, who conceived the idea of this study and who did most of the research, passed away on September 18, 1955.

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Blewett and Potzger (1950) stated that quadrat analysis of a small residual stand in Marion County at Fort Harrison near Indianapolis disclosed the structure of the stand to be very similar to that of the forest which the survey records indicated had existed over the two counties before settlement, a typical climax mixed mesophytic forest in which beech and sugar maple were the most important representatives. From their findings, the authors concluded that the association complex of the primeval forest is reflected in the structure of residual stands of little-disturbed forest.

Studies of the survey data from the central portion of the state (Blewett and Potzger 1950, Potzger and Potzger 1950) support the supposition of Potzger and Friesner (1940), based on considerable field data, with regard to the regional climax. The latter authors have shown that north-facing slopes and moist uplands support a modified beech-maple forest. South-facing slopes and ridgetops are typically occupied by oak-hickory stands. And intermediate slope exposures support a mixed mesophytic forest. Many workers have tended to oversimplify the distribution of forest types in the State by considering that the beech-maple forest is virtually restricted to the level till plains and that oak-hickory dominance starts rather abruptly below the glacial boundary. Potzger and Potzger (1950), however, using the survey records from a strip of counties in the west-central portion of the State, demonstrated that there is "no evidence of a sharp break between a mixed mesophytic forest cover in glaciated and oak-hickory in unglaciated areas. The data rather point to a mixed mesophytic forest in which the oak and hickory element is more prominent in rugged areas." In such rugged areas the predominant slope exposure determines which forest type is more abundant.

A study (Ross 1950) of the five southeasternmost counties revealed that, "the most abundant tree of the forest association was beech and the most prominently associated with it were sugar maple *(Acer saccharum)*, hickories (*Carya* spp.) and tulip popular *(Liriodendron tulipifera)*." The object of Ross' study, however, was to prove or disprove the contention that, contrary to popular opinion, *Pinus virginiana* had existed in Indiana prior to white settlement. Regardless of its sporadic distribution, the early surveyors had employed the pine as a witness tree on 14 occasions. Diameters of several of these trees implied an age which would have antedated even the earliest white settlement. Her study demonstrates the potential value of the survey records for clarifying problems of forest history and species distribution.

Three studies have analyzed the vegetation of those counties in the northwestern corner of the State which are included in or border on the prairie peninsula (Rohr and Potzger 1950, Finley and Potzger 1952, Potzger and Keller 1952). Vegetation maps compiled from the survey data are given in the first two of these papers. They illustrate the pattern of progressive change as one goes from forest to grassland. Traveling westward from the mixed mesophytic

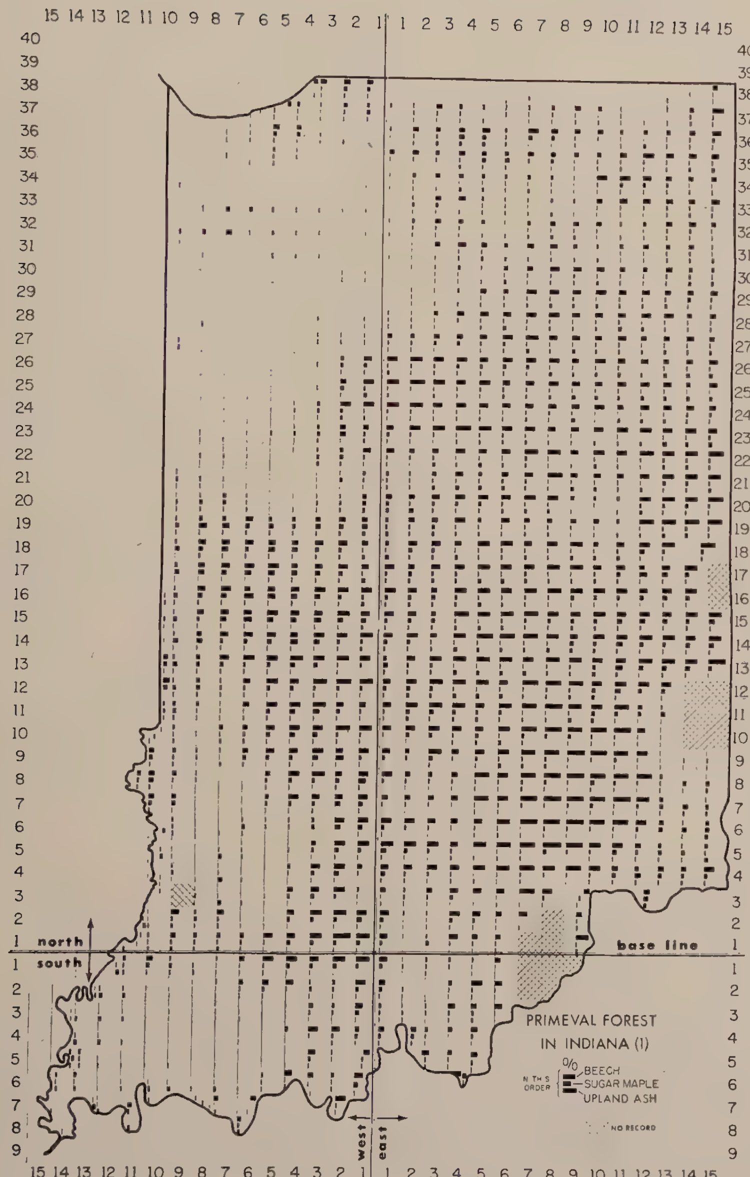


Fig. 1. Map-graph showing distribution in Indiana of the climax beech-sugar maple-upland ash forest association as percentages of total witness trees recorded by townships in the original U. S. Land Survey. (Copies of the tables of percentages on which this and figures 2 and 3 are based have been deposited in the Butler University Library, Indianapolis, Indiana.)

forest, the more mesic species, such as beech, maple, and ash, become less and less abundant and the more xeric oaks and hickories assume control of the crown. In the forest-grassland transition area, trees decrease both in number and size and oak opening and oak forests alternate with true prairie.

THE MAP-GRAPHS

The data compiled from the survey records were graphed, township by township, on three maps of the State (Figures 1, 2, 3). Percentages for beech *(Fagus grandifolia)*, sugar maple *(Acer saccharum)*, and the upland ashes *(Fraxinus americana, F. quadrangulata, Fraxinus* spp.) are shown in Fig. 1. Percentages for the upland oaks *(Quercus alba, Q. coccinea, Q. ellipsoidalis, Q. falcata, Q. muehlenbergia, Q. prinus, Q. rubra, Q. velutina)* and the hickories (*Carya* spp.) are shown in Fig. 2. Fig. 3 presents the combined percentages for beech, sugar maple, and upland ash, the combined perecntages of upland oak and hickory, and the combined percentages for all other species in each township.

In the western section of the State the bar graphs have been modified into a checkered pattern—derived from the vegetation maps in the prairie studies of the present series (Rohr and Potzger 1950 and Finley and Potzger 1952)—to indicate the distribution of savannah or oak-opening vegetation. In this same region, disjunct forest trees are denoted by dots. The dots are placed so that the first and last delimit the length of an imaginary percentage bar. The base map utilized for the map-graphs is somewhat stylized; the size and arrangement of the townships is, in reality, not quite so regular.

Survey records were not available for 17 townships. These include eight townships in two eastern areas which were included in the Ohio survey; eight townships of the George Rogers Clarke Reserve Land in the southeast; and one township in the Vincennes Donation Tract along the lower western border of the State.

The authors wish to express their appreciation to Mr. Jules Milette for aid in preparation of the map-graphs and to the Service de Biogeographie, Universite de Montreal, for his services.

TOPOGRAPHY AND PHYSIOGRAPHY OF INDIANA

Indiana has a land surface of more than 36,000 square miles (Visher 1922). Nearly 90 per cent of this area is situated between 500 and 1000 feet above sea level. The maximum elevation, which occurs in the east-central section, is 1285 feet. The minimum elevation, at the southwestern tip of the State, is 313 feet.

Approximately five-sixths of the State has been glaciated. The glaciated section, a part of the Central Lowland province of Fenneman (1938), is an area of small relief with broad areas of poor natural drainage (Visher 1922,

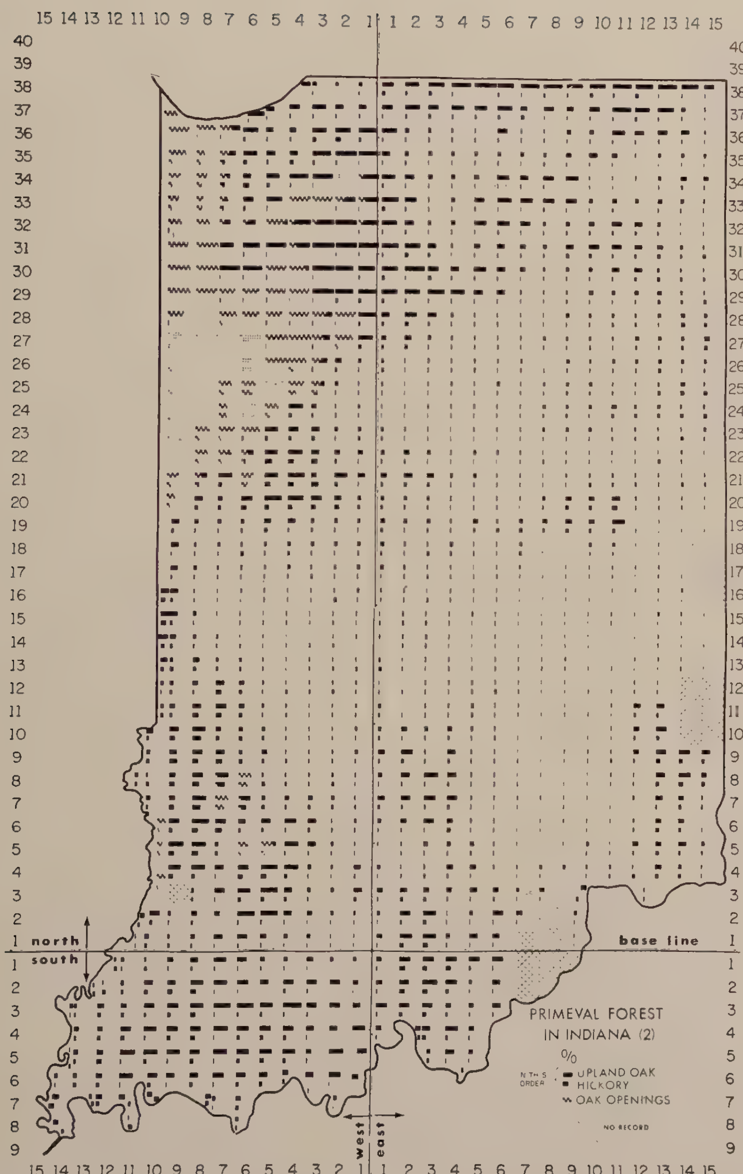


Fig. 2. Map-graph showing distribution in Indiana of the upland oak-hickory forest association as percentages of total witness trees recorded by townships in the original U. S. Land Survey.

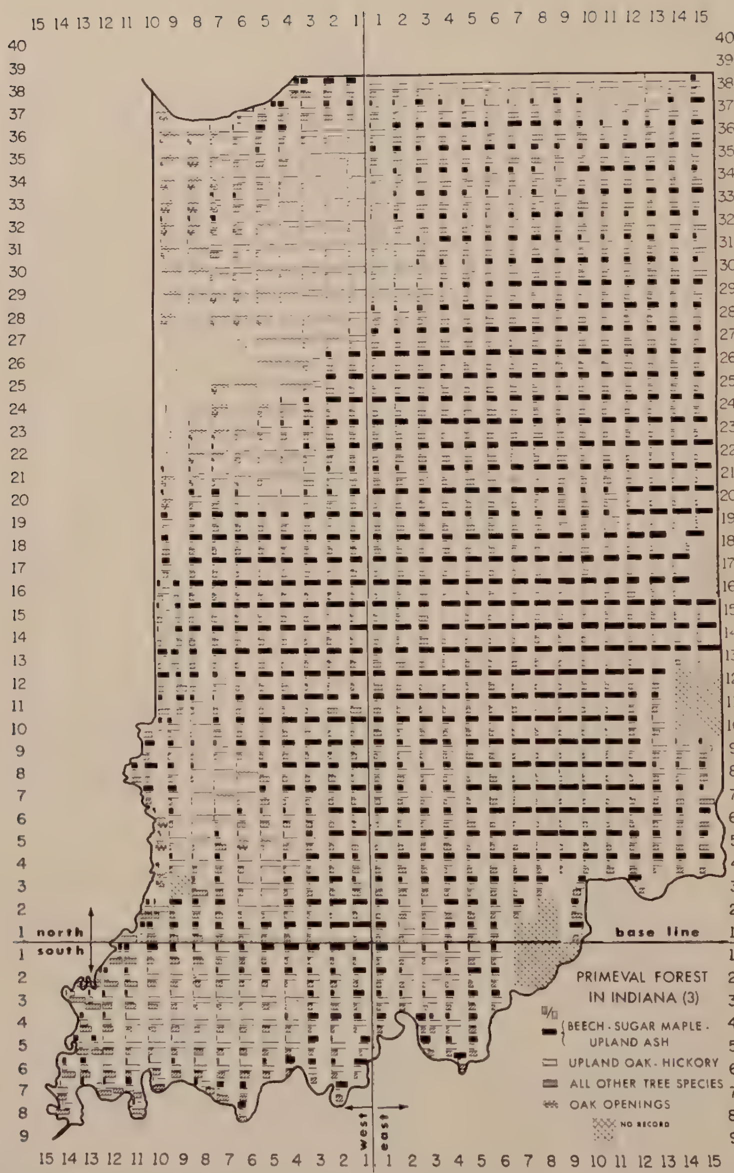


Fig. 3. Map-graph presenting summary of the primeval forest association in Indiana as combined percentages of beech-sugar maple-upland ash, of upland oak-hickory, and of all remaining tree species of total witness trees recorded by townships in the original U. S. Land Survey.

Bureau of the Census 1950). Throughout the northern quarter of the State there are frequent moraines and numerous glacial lakes. But the remainder of the glaciated section is "chiefly characterized by a covering of glacial till of nearly level surface without lakes and not well dissected by streams" (Malott 1922).

The unglaciated area comprises about 6000 square miles in the southwest and south-central portions of the State. In general, it has a diverse and broken topography. The more eastern portion of the area consists of a dissected upland famed for its forested hills or knobs. The western portion contains broad expanses of nearly level riverbottom and terrace lands.

DISCUSSION OF THE MAP-GRAPHS

Primeval Indiana was primarily a forested region. Only in the northwest, where the tall grass prairie extended into the State, did tree vegetation give way to extensive grassland (Figs. 1, 2, 3).

The open aspect of the prairie was reflected by the dearth of trees tallied in sixteen prairie townships. These townships had an average of ten witness trees each, in contrast to more than 200 in an average forested township. Absolutely no witness trees were recorded in three of the prairie townships (T25N, R8W; T26N, R8W; T26N, R7W).

Oak-opening vegetation bordered the true prairie (Fig. 2, 3). The savanna, in turn, gradually merged into the oak-hickory forest. The distribution of these various vegetation types and the transition from forest to grass land have been discussed by Rohr and Potzger (1950), Finley and Potzger (1952), and Potzger and Keller (1952).

The forest vegetation of Indiana was composed of two principal complexes, the beech-sugar maple-upland ash, or mixed mesophytic forest and the oak-hickory forest. In addition, various bottomland and transition associations occupied a considerable portion of the State.

Beech-Maple-Ash Forests. Townships in which at least 50 per cent of the witness trees were beech, sugar maple, and upland ashes, individually or in any combination, were considered to have been occupied by beech-maple-ash forests. Three hundred and ninety townships, 39 per cent of the total number considered, were covered by this type of forest (Figs. 1, 3). Most of these townships lie in a single block which occupies the central and eastern sections of the State.

Beech composed up to 80 per cent of the forest in some townships. But the contribution of the sugar maple never exceeded 40 per cent and that of the ashes did not exceed 19 per cent of the total number of stems in any township. Blewett and Potzger (1950), who analyzed the data from 25 townships in central Indiana, and Potzger and Potzger (1950), who tabulated the data from 57 townships in west-central Indiana, present a more complete picture of the composition of the beech-maple forest.

Oak-Hickory Forests. Townships in which at least 50 per cent of the witness trees were upland oaks and hickories are considered to have been covered by oak-hickory forests. These forests occupied large blocks of townships in the southern, southwestern, northwestern, and northern portions of the State (Fig. 2). In all, 280 townships, 28 per cent of the townships surveyed, were covered by oak-hickory forests. The composition of the association varied from place to place. Oaks comprised as much as 98 per cent of the stems in certain townships. Hickory rarely exceeded 40 per cent of the total number of stems and was commonly much less prominent.

Bottomland and Transition Forests. Bottomland and transition forests, in which neither oaks and hickories nor beech, sugar maple, and upland ashes aggregated as much as 50 per cent of the total number of witness trees, occupied one out of every three of the townships included in the survey. The fluctuations in abundance of these types throughout the State are indicated in Fig. 3 by the variations in lengths of the percentage bars representing "other tree species." Of course, these bars also include a varying proportion of understory and less common canopy species of the two major upland types. The composition of the primeval forests in two townships, one in southwestern and one in northwestern Indiana, in which bottomland hardwoods comprised more than 50 per cent of all witness trees is shown in Tables 1 and 2.

TABLE 1

Primeval forest composition in a southern Indiana township occupied primarily by bottomland hardwoods (T. 3 S., R. 13 W.—Gibson County). Figures indicate the percentage of land survey witness trees comprised by a given species.

Ulmus spp.	17.89%	*Gymnocladus dioica*	1.05
Liquidambar styraciflua	15.26	*Juglans nigra*	1.05
Acer saccharinum & *rubrum*	12.10	*Liriodendron tulipifera*	1.05
Fraxinus nigra	9.47	*Quercus bicolor*	1.05
Carya spp.	6.84	*Tilia americana*	1.05
Quercus alba	4.21	*Salix* spp.	1.05
Acer negundo	3.16	*Acer saccharum*	0.52
Celtis occidentalis	3.16	*Betula* spp.	0.52
Quercus velutina	3.16	*Carya illinoensis*	0.52
Platanus occidentalis	2.63	*Juglans cinerea*	0.52
Morus rubra	1.57	*Nyssa sylvatica*	0.52
Quercus rubra	1.57	*Sassafras albidum*	0.52
Cercis canadensis	1.05		

TABLE 2

Primeval forest composition in a northern Indiana township occupied primarily by bottomland hardwoods (T. 30 N., 15 E.—Allen County). Figures indicate the percentage of land survey witness trees comprised by a given species.

Fraxinus nigra	26.40%	*Quercus macrocarpa*	5.06
Ulmus spp.	15.17	*Acer saccharum*	3.92
Fagus grandifolia	10.67	*Quercus rubra*	3.37
Carya spp.	9.55	*Platanus occidentalis*	2.24
Fraxinus spp.	9.55		

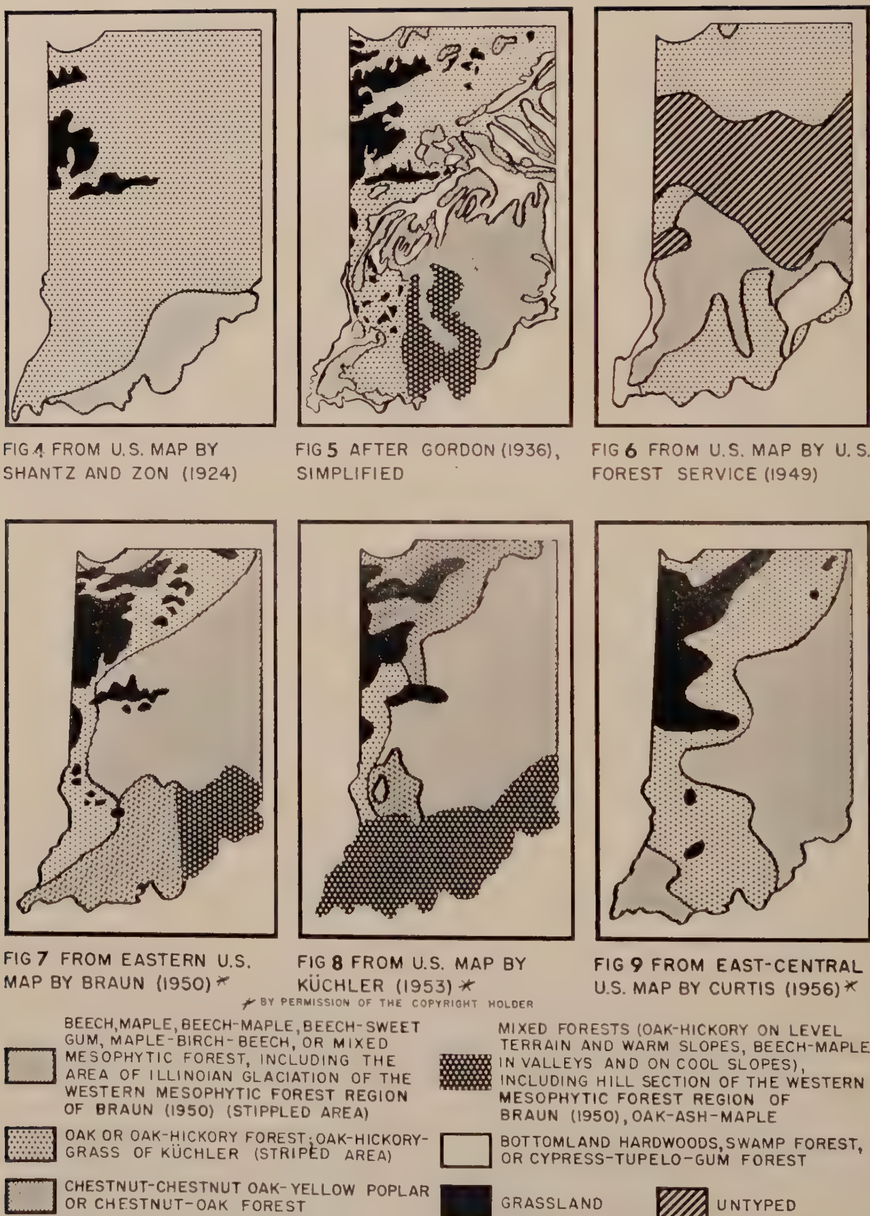
PREVIOUS INTERPRETATIONS OF INDIANA VEGETATION

From the records of the original United States Land Survey it is apparent that beech-maple-ash forests occupied the central and eastern portions of Indiana. These forests were enclosed on the south, southwest, northwest, and north by oak-hickory forests. In the northwest quarter of the State, the oak-hickory forests became more sparse, forming an oak-opening vegetation and thence gave way to tall grass prairie (Figs. 1, 2, 3). It is of interest to compare these irrefutable records of the composition and distribution of Indiana vegetation with the interpretations of several modern workers. These interpretations can be divided into three categories:

Interpretations which depict Indiana as covered by deciduous forests. This "noncommittal" interpretation is often used in small scale maps of the vegetation of the United States or of the North American continent. Examples are included in papers, such as those by Shreve (1917), Livingston and Shreve (1921), Shelford, Jones, and Dice (1926) and Pitelka (1941), in text books, such as those by Weaver and Clements (1938) and Transeau, Sampson and Tiffany (1940), and in maps published by the United States Forest Services (1948).

Interpretations which depict Indiana as covered principally by oak-hickory forests. Shantz and Zon (1924) compiled a map of the vegetation of the United States which, even today, is unexcelled for inclusiveness and detail. However, Raphael Zon, who was responsible for mapping the forest regions, grossly misinterpreted Indiana's forests by mapping all but the southeastern portion as oak-hickory forest (Figure 4). In the text, the authors state, "In the western part of the oak region embracing western Ohio, Indiana, Missouri, and Oklahoma, and largely bordering on the prairies, the chestnut, chestnut oak, and yellow poplar gradually disappear and the forest becomes characteristically an oak-hickory forest."

The southeastern section of Indiana was mapped by Zon as chestnut-chestnut



Figs. 4—9. Selected maps showing previous interpretations of Indiana vegetation.

oak-yellow poplar forest. From the Land Survey records, it is obvious that the boundary of this area is entirely erroneous. The section actually contained a large portion of beech-maple forest as well as a smaller amount of oak-hickory forest. Ross (1950), working from the Survey data, stated that in the five southeasternmost counties of the State, "The most abundant tree of the forest association was beech and the most prominently associated with it were suger maple *(Acer saccharum)*, hickories (*Carya* spp.) and tulip poplar (*Liriodendron tulipifera*)."

The interpretive errors in the Shantz and Zon map have been perpetuated by the extensive use of the work by authors of scientific papers (e.g., McDougall 1925, Huffaker 1942) and of text books (e.g., Davis 1943; Goode 1950; Kroeber 1953). Zon (1941), in a later, simplified map did not attempt to correct his classificatory error. Rather than that, he characterized the entire forested area of the State as "oak" forest. Dayton (1949), writing for the U. S. Forest Service in the *Yearbook of Agriculture,* copied the Shantz and Zon map without correction or criticism.

Den Uyl (1954), after studying figures pertaining to the annual hardwood lumber production in Indiana from 1869 to 1915, incorrectly concluded that Indiana's "old growth forests were predominantly oak." He further misconceived that, "These figures would indicate that . . . the 'beech-maple' association must have occupied a minor position or must have been very much restricted in area." Den Uyl attempts to discredit the fact that many recent ecological analyses (Esten 1932, Potzger and Friesner 1940, Braun 1950) have shown the beech-maple type to be wide-spread and of prime importance in the State by assuming that, " . . . it is probable that when the early ecologists came into Indiana and our neighboring states they did see residual stands in which beech and maple could easily have been prominent. The lumber production records clearly indicate that the oaks were the favored trees to be cut and hence . . . one's observations would put beech and maple into the ecological picture."

Interpretations which depict Indiana as covered by oak-hickory and beech-maple forests. Perhaps the first map to indicate the prominence of beech-maple forests in Indiana was published by Shelford (1931). Shelford's map, however, is apparently little more than an adaptation of the Shantz and Zon map (1924). In his revision, Shelford substituted the name "beech-maple" for the former classification, "oak-hickory." The prairie area was virtually unaltered. The chestnut-chestnut oak-yellow poplar type in the southern portion of the State was retermed "oak-chestnut" forest and its limits were extended slightly to the west.

Gordon (1932), who supplemented field studies with data culled from the early surveyor's records, compiled a map of the natural vegetation of the east-central states. Two tongues of prairie grassland were shown to project into the

northwestern section of Indiana. Oak-hickory forests were indicated throughout the north, west, and in a portion of the southwest sections. Beech-maple forests were mapped in the entire central and eastern sections and also in the southwestern section. An oak-chestnut type was shown to occupy a long, narrow area oriented longitudinally along the southern quarter of the long axis of the State. This distribution is very similar, in its gross aspects, to the distribution determined in the present study.

Kendeigh (1934) indicated that the entire State, with the exception of a small section in the northwest, was occupied by beech-maple forests. However, by an overprinted symbol, he also indicated widely distributed oak-hickory forests.

In 1936, Gordon published a detailed "Preliminary Vegetation Map of Indiana" based on observations made during trips throughout the State (Fig. 5). Eight vegetation units were recognized: prairie grassland, upland oak forest, northern swamp forest, beech forest, mixed forest, beech-sweet gum forests, southern swamp forest, and bald cypress forest. Except for variations introduced by considerable dissection due to subdivision, the general distribution of oak-hickory and beech-maple forests remained the same as shown in his previous map (Gordon 1932). The map is especially notable in that it shows that scattered prairie patches existed far to the north, east and south of the main prairie projections. Mapping of the "prairie counties" correlates extremely well with maps compiled from the Survey Records by Rohr and Potzger (1950) and Finley and Potzger (1952). The manuscript of Gordon's map served as the source of data for the distribution of Indiana prairie areas shown in Transeau's map of the "Prairie Peninsula" (1935).

It is beyond the scope of this paper to evaluate the validity of categorization of Gordon's other forest types or the accuracy of the mapping of those types. Potzger and Friesner (1940), however, considered that Shantz and Zon (1924) had "classified the State too dry and Gordon (1936) [had classified it] too mesophytic." McCoy (1939) indicated that Gordon's interpretation of forest-type distribution in southwestern Indiana may also be incorrect.

Potzger (1935) candidly summarized the findings of his intensive field studies of a small area near Bloomington, Indiana: "The most outstanding single feature of the upland forest, however, is the dual nature of the forest type. The transition from beech-maple on the north-facing slopes to oak-hickory on the south-facing slopes is not gradual but abrupt and decisive, marked by a sharp line along the ridge."

Later, on the basis of extensive quadrat data collected in lower central Indiana, Potzger and Friesner (1940) found this situation to be general throughout the area. They reported that "In all the counties studied the two forests types customarily termed *Acer-Fagus* and *Quercus-Carya* are sensitively bal-

anced, . . ." and concluded that "apparently the climate favors a modified *Acer-Fagus* climax, and microclimate induced by topography causes and maintains the *Quercus-Carya* forest cover type in central Indiana."

Potzger and Friesner (1940) also emphasized that the common designation, maple-beech type, "must be made very inclusive of many other species which play a part in the crown cover when Indiana forests of this type are considered." They concurred with Braun (1938) who suggested that Indiana beech-maple forests are actually representatives of "the 'mixed mesophytic association' in which beech and maple are the most prominent members."

Seven categories of native vegetation were mapped by the Indiana Soil Survey (1941). According to its compilers, "this map does not outline vegetation areas, but rather characterizes soil regions as to vegetation." It is difficult to evaluate this map or to compare it with the land-survey data because of the peculiar categories employed. For example, one category lumps "oak-hickory, beech-maple, ash-elm, tulip, walnut," another is comprised of "pin oak-sweet gum: beech-maple: oak-hickory," and a third category includes "chestnut, scarlet, black, white, and red oaks: maple, beech, hickory, tulip, walnut, scrub pine." The distribution of predominantly-grass vegetation in the northwestern section appears to be in close agreement with the distribution recorded by the original surveyors. The importance of floodplain and swamp forests along the Wabash, White, and Whitewater Rivers, however, is perhaps overemphasized.

Kittredge (1948) revised the Shantz and Zon map (1924) or a later modification of it. His map depicts Indiana as covered primarily by oak-hickory forests. However, an arm of the "birch-beech-maple-hemlock forest" is shown to project into the east-central portion of the State. Following Shantz and Zon, Kittredge mapped southern Indiana as "oak-chestnut-yellow poplar." He also mapped small areas of tall grass prairie in the northwest and "riverbottom hardwoods and cypress" in the extreme southwest and northeast portions of the State.

The recent United States Forest Service map (1949), "Areas characterized by major forest types in the United States," is in general agreement with the Indiana land survey (Figure 6). Several points of disagreement, however, are obvious. On the Forest Service map the entire northern third of the State is typed as oak-hickory. The survey data indicate that this area was divided between oak-hickory (in the west and extreme north), beech-maple (in the central and southeastern portions), and bottomland forests in the central and eastern portions) (Fig. 3). Oak-hickory is also shown by the Forest Service to occupy virtually the entire unglaciated section. This is in general agreement with the survey data (Fig. 2), but the importance of the association along the western edge of the State was ignored by the Forest Service.

Beech-maple forests are shown by the Forest Service map to occupy a strip

of land extending across the southern half of the central portion of the State. This band is narrow at the east and broad at the west. Finger-like projections extend into the southwestern and southern portions. But the land survey records show that the beech-maple type actually occupied a wide area in the east-central and southeastern portion of the State which abruptly narrowed to the west (Fig. 1). An arm of beech-maple did extend to the south, but not to the southwest. The Forest Service map shows bottomland forests to occupy a narrow strip along the southwestern border of the State. The land survey data (Fig. 3), however, do not support the contention that the type was of great importance very far north of the confluence of the Wabash and White Rivers. And the survey data illustrate that the large area in the southeastern portion of the State shown by the Forest Service map to be bottomland forest is actually an area in which beech is especially prominent.

Braun's recent (1950) book on the deciduous forests of eastern North America presents a remarkably accurate picture of the distribution of oak-hickory and beech-maple forests in Indiana. Braun's map (Figure 7) shows that the former type occupies the entire northern and western sections of the State, while the latter covers the central and eastern sections. The Hill Section of the Western Mesophytic Forest Region is shown to occupy the west-central portion of southern Indiana. "Vegetationally, this is an area of mixed forests—usually some phase of mixed mesophytic forest on northerly slopes, and of oak or oak-hickory forest on drier slopes and ridges" (Braun 1950). The southeastern section is characterized as the Area of Illinoian Glaciation of the Western Mesophytic Forest Region. "The drier slopes and exposed river bluffs [in this section] display remnants of an oak-ash-maple forest . . . . On less dry slopes and in maturely dissected places, forest development has progressed to a mixed mesophytic forest climax." (Braun 1950). On flats, "Pin oak, sweet gum, red maple and white elm separately, and in various combinations, together with some accessory species as swamp white oak, sour gum, white oak, shell bark hickory, and beech compose the developmental forest stages. In secondary forests, pin oak and/or sweet gum frequently dominate. The hydrarch succession of the undissected flats terminates in a beech forest, which is here a physiographic climax. Sugar maple is not a part of this community" (Braun 1950). The validity of this last statement is witnessed by the fact that in most of the townships in the southeastern section which are regarded as beech-maple in the present study, beech alone comprised more than 50 per cent of the witness trees (Fig. 1). Distribution of prairie areas is obviously adapted from Gordon (1936).

In a map embodying his physiognomic system of classification, Küchler (1953) presents a clear picture of the distribution of various forms of vegetation throughout the United States. His physiognomic types are divided into floristic types. Five floristic types are shown to occur in Indiana (Figure 8). Beech-maple forests are indicated throughout most of the northeastern quarter

of the State. However, the association is too abruptly terminated on the west and its extreme importance in the southeastern portion of the State is ignored.

Oak-hickory forests are shown only in the central-western portion of Indiana. But according to the survey data, this area was occupied by beech-maple forests (Fig. 1). The extensive body of oak-hickory in the southwestern section is not indicated. And the true oak-hickory forests in the northern portion of the state are included in an area characterized by Küchler as oak-opening type (oak-hickory-bluestem [in patches]). A large block of oak-openings is shown to occur in the lower central-western section. According to the survey data, a small patch did occur in this area (Fig. 2), but it was far less extensive than that mapped by Küchler.

Almost the entire southern third of the State is typed as oak-ash-maple [mixed] forest. According to the survey data, however, the western half of this area was primarily covered by oak-hickory forests (Fig. 2), while the eastern half was occupied mostly by beech-maple forests (Fig. 1). There was some interdigitation.

In his map of the "Vegetation of North Central United States," Curtis (1956) presents a generalized, but fairly accurate representation of the forest distribution in Indiana (Figure 9). Curtis employed only two forest types, a "maple climax" and an "oak subclimax." The maple climax is shown to occupy the central and eastern areas. The oak subclimax occupies a narrow strip from the northwestern corner diagonally through the State to the southwestern and thence to the central southern border. "Maple Climax" is also shown to occupy the southwestern tip of the State. The Survey data, however, indicate that sugar maple was virtually absent from this area (Map 1).

SUMMARY

Records of the original land survey of Indiana reveal that, prior to settlement, the State was primarily covered by deciduous forests. These forests were composed of two major complexes, a mixed mesophytic forest in which beech and sugar maple were usually outstanding and an oak-hickory forest. The former type, which covered at least 40 per cent of the area, occurred primarily in a single block which occupied the central and eastern sections of the State. The oak-hickory type covered about 30 per cent of the State. It occupied peripheral areas to the south, southwest, northwest and north of the beech-maple. Approximately 32 per cent of the townships in the State were either occupied by nearly equal mixtures of beech-maple and oak-hickory forests or they were occupied by forests in which other species were predominant.

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